Universidad Politécnica de Madrid

Escuela Técnica Superior de Ingeniería de Montes, Forestal y del Medio Natural

Efectos e interacciones del clima, la estructura y la gestión sobre el crecimiento de los árboles y la dinámica de especies en ecosistemas forestales

Tesis Doctoral

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Ingeniero Forestal

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Resumen

En las últimas décadas han ocurrido grandes cambios que han afectado a las masas forestales españolas. Por un lado, ha habido un aumento de las temperaturas y de los eventos climáticos extremos (sequías y heladas tardías) y por otro un abandono de las prácticas selvícolas tradicionales como consecuencia de la disminución de las rentas obtenidas del monte, y en general del ámbito rural con el consiguiente despoblamiento de las zonas rurales, así como de los cambios en la sociedad, la cual valora crecientemente la preservación de los ecosistemas naturales. En este trabajo estudiamos el impacto que están teniendo estos cambios sobre los bosques de montaña españoles. Debido a su mayor sensibilidad, se ha prestado especial atención a aquellas especies típicas de bosques templados que encuentran en la Península Ibérica su límite de distribución meridional. Se ha muestreado dos espacios naturales protegidos, el Parque Nacional de los Picos de Europa y el hayedo de Montejo de la Sierra, y cuatro especies arbóreas, *Fagus sylvatica*, *Quercus petraea*, *Quercus pyrenaica* y *Betula pubescens*. En los análisis se han empleado fundamentalmente técnicas dendrocronológicas, las cuales están basadas en el análisis de los anillos de crecimiento que quedan registrados en la madera de los árboles. En Picos de Europa la dinámica de *F. sylvatica* y *Q. petraea* ha estado vinculada a lo largo de los últimos 100 años a sucesos de mortalidad aislados asociados a eventos climáticos extremos, lo que ha favorecido a *F. sylvatica*, más adaptada a la competencia que *Q. petraea*. En El Hayedo de Montejo el factor que más ha influido sobre el crecimiento a largo plazo es el aumento de la espesura, que ha provocado el decaimiento del crecimiento en *Q. petraea* y especialmente en *Q. pyrenaica*. Estas especies se podrían ver desplazadas, si no se aplican medidas selvícolas que reviertan el proceso, por *F. sylvatica*, aunque esta última es mucho más sensible que *Q. petraea* y *Q. pyrenaica* frente a las heladas tardías, que podrían ser cada vez más frecuentes como consecuencia del cambio climático.

Abstract

In recent decades the Spanish forests have been affected by major changes. On the one hand, there has been an increase in temperatures and extreme climatic events (droughts and late frosts) and, on the other hand, there has been an abandonment of traditional uses as a consequence of the decrease in the income obtained from the forest, and in general from the rural environment, with the consequent depopulation of rural areas, as well as increasing concern about the preservation of natural ecosystems of society. In this work we study the impact that these changes are having on Spanish mountain forests, paying special attention to those species typical of temperate forests that have their southern limit of distribution in the Iberian Peninsula due to their greater sensitivity. Two protected natural areas, the *Picos de Europa* National Park and the *El Hayedo de Montejo* forest, and four tree species, *Fagus sylvatica*, *Quercus petraea*, *Quercus pyrenaica* and *Betula pubescens*, were sampled. Dendrochronological techniques have been used to analyze the effects of climate and stand structure on tree ring growth and characterize species response and forest dynamics. In *Picos de Europa*, the dynamic of *F. sylvatica* and *Q. petraea* have been linked over the last 100 years to isolated mortality events associated with extreme climatic events, which has favored *F. sylvatica*, more adapted to competition than *Q. petraea*. In the *El Hayedo de Montejo* forest, the stand density increase has been the most influential factor in long-term growth, which has caused a decline in the growth of *Q. petraea* and especially *Q. pyrenaica*. These species could be displaced, if no silvicultural traits are applied to reverse the process, by the competition-tolerant *F. sylvatica*. Nevertheless, *F. sylvatica* is much more sensitive than *Q. petraea* and *Q. pyrenaica* to late frosts, which could become increasingly frequent as a result of climate change, so a strategy to enhance forest resilience would be maintaining mixed stands.

CAPÍTULO 1. INTRODUCCIÓN GENERAL

La cuenca mediterránea, y especialmente España, es una de las áreas de mayor diversidad del mundo, con una flora vascular diversa y rica en endemismos y abundancia de hábitats (Myers et al., 2000). En sus ecosistemas montañosos se entremezclan frecuentemente especies típicamente mediterráneas con especies características de bosque templado que encuentran en España, y en general en el norte de la cuenca mediterránea, su límite de distribución meridional, lo que hace que con frecuencia se encuentren en condiciones climáticas ~~límite~~ extremas para ellas, en relación con las temperaturas de las poblaciones más septentrionales. Esto hace que estos ecosistemas montañosos sean especialmente sensibles a los cambios del medio, especialmente del clima.

Los factores que más influyen tanto sobre el crecimiento individual de los árboles, y por tanto sobre su vitalidad, como sobre la dinámica de los ecosistemas arbóreos son: las perturbaciones, de origen natural (como los incendios) o antrópico, (como los tratamientos selvícolas); el suelo, elemento que varía a medio plazo, por el enriquecimiento anual de sus perfiles por el desprendimiento de sus partes aéreas y radicales con crecimiento primario; el clima, que presenta tres escalas de variación, intraanual, que permite la ocurrencia de las estaciones y los ciclos biológicos (crecimiento/parada vegetativa), interanual a corto plazo, con la variabilidad típica de los sistemas estocásticos, e interanual a largo plazo, en la que se incluyen procesos de origen natural o antrópico como el cambio climático; y las características de la masa arbórea como son la composición, la estructura y la densidad. Tanto el clima como la gestión forestal (que afecta directamente a la estructura y densidad de las masas forestales) han sufrido una serie de cambios en las últimas décadas que han influido sobre el crecimiento, vitalidad y dinámica de las masas forestales.

1.1. Clima

Desde mediados del siglo XX se ha producido un aumento general de las temperaturas, siendo los últimos 30 años los más cálidos desde 1850, año en que se inician los

registros periódicos, donde la cuenca mediterránea, y específicamente España, han sido una de las áreas más afectadas (IPCC, 2014). Aunque las precipitaciones medias anuales se mantienen estables, su distribución sí ha cambiado, reduciéndose durante el periodo estival. Estas variaciones han afectado al crecimiento de las masas forestales y hay abundantes investigaciones que relacionan tendencias del crecimiento negativas (y por tanto menor productividad) con el aumento de las temperaturas, tanto en bosques mediterráneos (Camarero et al., 2015; Gea-Izquierdo et al., 2014; Macias et al., 2006; Sarris et al., 2011, 2007) como en bosques templados que crecen bajo la influencia del clima mediterráneo (Colangelo et al., 2017; Dorado-Liñán et al., 2017; Piovesan et al., 2008). Además, las proyecciones de cambio climático para la región mediterránea, basadas en simulaciones de modelos climáticos globales y regionales, muestran un panorama de disminución de las precipitaciones estivales y aumento general de las temperaturas. En un escenario con emisiones intermedias de CO_2, se estima que la disminución de las precipitaciones anuales superará el 15% y que el aumento de las temperaturas alcanzará los 3,6 °C a finales del siglo XXI (Jacob et al., 2014). De acuerdo con las proyecciones climáticas la Península Ibérica sería el área más sensible y donde mayores caídas en la productividad de las masas forestales se van a producir de toda Europa (Morales et al., 2007; Reyer et al., 2014).

Por otro lado, el cambio climático puede aumentar la frecuencia de los eventos meteorológicos extremos como las sequías o las heladas tardías, desafiando la capacidad de las especies arbóreas, que suelen tener una larga vida y un ritmo de evolución lento, para adaptarse localmente (Alberto et al., 2013).

Las sequías, además de reducir la productividad, pueden debilitar al arbolado, llegando a producir episodios de mortalidad, que en casos extremos pueden llevar a la sustitución de una especie por otra más competitiva o tolerante a la sequía (Martin et al., 2015; Pederson et al., 2014; Sangüesa-Barreda et al., 2015; Suárez et al., 2004). Sin embargo, estos episodios de mortalidad no tienen por qué suponer un impacto negativo para el ecosistema. Tanto en los bosques propensos a la sequía como en los templados, las variaciones climáticas interanuales pueden ser uno de los principales factores que determinan su dinámica. La mortalidad de los árboles causada por los periodos de sequía, genera claros en la masa que son ocupados por la regeneración de

los árboles durante los periodos húmedos y frescos (Villalba and Veblen, 1997). De este modo, la sequía elimina los individuos de más edad o menos vigorosos y favorece el establecimiento de la regeneración de la misma especie arbórea o de especies diferentes con requerimientos contrastados (Brown and Wu, 2005). No obstante, en casos extremos, las sequías pueden llegar a desencadenar procesos masivos de mortalidad en el arbolado, los cuales aparentemente están aumentando de frecuencia como consecuencia del cambio climático (Allen et al., 2010).

La ocurrencia de heladas tardías, es decir, temperaturas bajo cero que se producen tras el inicio del periodo vegetativo, también está variando en las últimas décadas. Aunque esta variación no es uniforme, sino que depende de las zonas geográficas, se ha producido en general un aumento en Europa desde 1959 (Ma et al., 2019; Zohner et al., 2020). Las heladas tardías son eventos que pueden llegar a causar grandes daños a los ecosistemas forestales, como reducciones abruptas de la productividad, mortalidad y cambios en la composición de las especies (Augspurger, 2011, 2009), especialmente si se convierten en algo frecuente debido al cambio climático (Körner et al., 2016). A escala de árbol, una helada tardía puede dañar las hojas, afectando a su morfología, fisiología y composición química (Klosson and Krause, 1981a, 1981b; Sakai and Larcher, 1987). Las raíces y los tejidos vivos del tallo están aislados por el suelo y la corteza exterior, respectivamente, y es menos probable que sufran daños. Cuando la helada es de la intensidad suficiente, ésta mata a las hojas, obligando a los árboles a rehacer el follaje utilizando los carbohidratos no estructurales y los nutrientes minerales almacenados. Sin embargo, esta segunda cohorte de hojas puede retrasarse hasta un mes o más con respecto a la primera (Nolè et al., 2018), produciéndose la pérdida de fotosíntesis. Además, esta segunda cohorte de hojas puede ser menos productiva debido a menores concentraciones de nutrientes de la hoja, tamaño de hoja más pequeño y/o un número total de hojas reducido (Awaya et al., 2009). La escasa ganancia de carbono y la reposición parcial de las reservas podría reducir el crecimiento e incluso esta limitación de carbono podría hacerse crónica afectando a la resiliencia del arbolado, es decir, su capacidad de recuperación tras un impacto.

1.2. Gestión, competencia y estructura forestal

El otro de los factores con importancia sobre el crecimiento es la gestión forestal y, con ella, la espesura y la estructura de las masas (Camarero et al., 2011; Linares et al., 2009). En las últimas décadas, la política forestal en Europa se ha orientado hacia la llamada gestión forestal próxima a la naturaleza, aumentando considerablemente el área incluida en espacios naturales y ordenada con fines de conservación, a lo que hay que añadir el abandono generalizado de algunos usos tradicionales debido al bajo valor económico de los recursos forestales (Moreno-Fernández et al., 2016) y a la despoblación de las zonas rurales. Sin embargo, la mayoría de los bosques europeos tienen una larga historia de transformaciones antropogénicas (Schoolman et al., 2018; Valbuena-Carabaña et al., 2010) y, debido a ello, suelen ser relativamente jóvenes. Además, durante las últimas décadas los bosques en Europa han ido colonizando nuevos terrenos gracias a las repoblaciones, al abandono de los terrenos agrícolas menos productivos y de las prácticas ganaderas tradicionales, así como al calentamiento del clima en los límites de distribución septentrionales (Álvarez-Martínez et al., 2014; Penniston and Lundberg, 2014; Price et al., 2017); estando todos estos nuevos bosques también en etapas sucesionales tempranas. El hecho de que la mayoría de las masas forestales europeas sean relativamente jóvenes, sumado a la reducción o eliminación de las prácticas selvícolas, está provocando que, debido a la propia dinámica natural, haya un aumento con el tiempo de la espesura de los bosques y de la competencia entre los árboles, lo que puede provocar una disminución en el crecimiento (Hosseini et al., 2018; Linares et al., 2010; Ruiz-Benito et al., 2013; Voelker et al., 2008).

Por otra parte, la dinámica natural en masas mixtas puede llevar, aparejado al aumento de la espesura, a la sustitución de las especies de luz por aquellas más competitivas (que pueden sobrevivir y crecer con altas densidades) y tolerantes a la sombra. Un claro ejemplo son los bosques donde se mezcla el haya con las distintas especies de roble, en los cuales la tendencia de la dinámica natural es formar masas monoespecíficas de haya, donde los robles son desplazados a las zonas rocosas con menor profundidad de suelo (Petritan et al., 2017), debido a la mayor tolerancia a la sombra del haya, su mayor producción de semillas (Harmer, 1994), que le permite

ocupar antes los sitios con mejor suelo, y su mayor capacidad para crecer con altas espesuras (del Río et al., 2014; Gazol and Ibáñez, 2010).

1.3. Estudio de los efectos del clima y la gestión forestal en los ecosistemas forestales a través de la dendroecología

Casi todos los trabajos realizados para el desarrollo de esta tesis se encuadran dentro de la dendrocronología, la ciencia encargada de la datación, medición y análisis de los anillos de crecimiento de las especies leñosas (Fritts, 1976) y del estudio de los factores que influyen sobre ellos, especialmente el clima. La metodología habitual empleada dentro de esta disciplina consiste en extraer dos muestras de madera en cada árbol con barrena de Pressler, que posteriormente son pegadas en listones de madera para facilitar su posterior lijado. En el lijado se utilizan diferentes grosores de grano hasta que los anillos son claramente visibles (**Fig. 1.1**). Uno de los aspectos metodológicos más importantes de la dendrocronología es la correcta datación de los anillos. Sabiendo la fecha en la que se han tomado las muestras, se va retrocediendo en la serie de anillos y asignando a cada uno de ellos el año durante en el que se formó. Debido a que es frecuente encontrarse anillos casi imperceptibles, dobles o años en los que no se formó un anillo, para asignar correctamente el año es necesario hacer datación cruzada, consistente en sincronizar las series de crecimientos de manera visual (haciendo coincidir los años característicos), gráfica (haciendo coincidir los patrones de crecimiento) y estadística (maximizando las correlaciones entre series de crecimientos). La medición de los anillos se realiza directamente mediante plataformas de medición lineal (**Fig. 1.2**) o con determinados programas de ordenador tras el escaneado de las muestras. Una vez obtenidas las cronologías de crecimientos la metodología a seguir depende de los objetivos buscados. Si se quiere estudiar la variabilidad a medio y largo plazo, los crecimientos radiales se convierten en área basimétrica, la cual se comporta de una manera más estable con el tiempo. Por el contrario, si se quiere estudiar la variabilidad anual, se procede a la estandarización de los crecimientos, generalmente ajustando funciones polinómicas por intervalos (*splines*) y posteriormente una función de autocorrelación, para eliminar por un lado el

efecto aquellos factores que influyen en el crecimiento a largo plazo, como la edad, la espesura o la tendencia del clima, y por otro la propia autocorrelación de los crecimientos. Finalmente se construyen series medias de cada sitio a partir de los crecimientos estandarizados o crecimientos en área basimétrica.

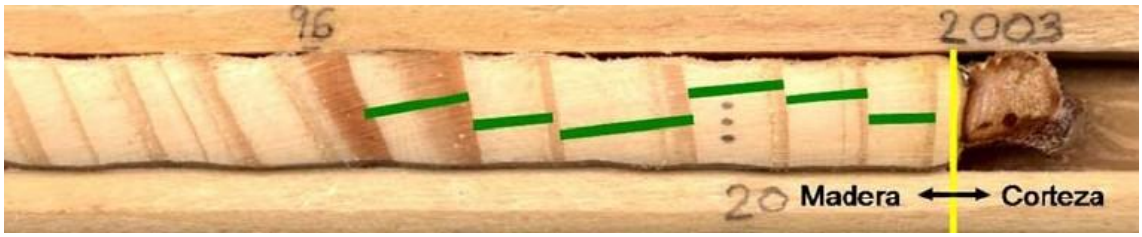

Figura 1.1. Testigo de madera pegado, pulido y datado sobre un soporte de madera. El último año de crecimiento todavía sin acabar es el 2003, justo debajo de la corteza. Fuente: Gutiérrez (2009).

Figura 1.2. Plataforma LinTab (Rinntech, Heidelberg, Alemania) de medición lineal de anillos de árboles para discos de tronco y testigos de madera. Fuente: https://rinntech.info/products/lintab/.

La dendrocronología se basa en cuatro principios (Speer, 2012): principio del uniformismo, principio de los factores limitantes, principio de la datación cruzada y principio del crecimiento agregado de los árboles. El principio del uniformismo supone que los procesos biológicos y físicos que en la actualidad determinan el crecimiento de los árboles han operado de la misma manera en el pasado y operarán de igual manera en el futuro, de manera que unas condiciones ambientales determinadas que producen en la actualidad una respuesta concreta en los árboles también habrán provocado o provocarán la misma respuesta si dichas condiciones se han dado en el pasado o se dan en el futuro (Gutiérrez, 2009). El principio de los factores limitantes supone que del conjunto de factores que intervienen en el proceso de crecimiento de los árboles, siempre suele haber uno que limita el proceso. Así, cuando se analizan anillos que presentan una sincronía, ésta es debida al efecto de algún factor limitante común (Gutiérrez, 2009). El principio de la datación cruzada supone que los árboles que han crecido bajo unas mismas condiciones climáticas mostrarán un patrón de variación común, normalmente como resultado de uno o unos pocos factores limitantes comunes (Gutiérrez, 2009). El principio del crecimiento agregado de los árboles supone que la variabilidad de los crecimientos anuales está explicada por la combinación de los factores intrínsecos al árbol (como la edad y el tamaño), el clima y las perturbaciones.

La primera cita en la que se menciona la formación de anillos anuales por las plantas leñosas se ha atribuido a Teofrasto en el 322 a. C., filósofo y botánico griego contemporáneo de Aristóteles (Studhalter 1956). Hasta el siglo XIX solo hay citas puntuales a los anillos de los árboles, difundiéndose su estudio durante este siglo, aunque todavía de un modo muy incipiente (Speer, 2012). Será a principios del siglo XX cuando Douglass, desde Estados Unidos, inicie el desarrollo de la dendrocronología como disciplina independiente que requiere la utilización de métodos específicos. Los primeros estudios se centraron en la arqueología (dendroarqueología), datando objetos de madera (desde estructuras de edificaciones a piezas de instrumentos musicales) mediante la sincronización de los anillos, y en la climatología (dendroclimatología), estimando el clima pasado en función del tamaño de los anillos que se crearon bajo esas condiciones. Posteriormente surgirán las aplicaciones ecológicas (dendroecología), que son las empleadas en la presente tesis, como el

estudio de los incendios, plagas, vecería, perturbaciones, sequías, heladas, relaciones crecimiento-clima o crecimiento-espesura, etc.

En el desarrollo de la tesis se emplean diferentes métodos para conocer las relaciones crecimiento-clima de las masas forestales, lo que nos permite evaluar su vulnerabilidad al cambio climático. Mediante el estudio de los anillos analizamos también las perturbaciones pasadas, los periodos en los que se instaló regenerado de las diferentes especies arbóreas, la dinámica y los cambios en la capacidad competitiva, adaptación y vitalidad de las especies, gracias a lo cual podemos proyectar su evolución futura en función de los posibles escenarios climáticos.

1.4. Objetivos generales

Entender y predecir las consecuencias de los cambios que se han dado en las últimas décadas en el clima y la gestión es uno de los retos actuales de la ciencia forestal. El estudio de la respuesta de los bosques frente a estos cambios recientes nos permitirá conocer su grado de adaptación y resiliencia, predecir el impacto de los cambios que continuarán durante las próximas décadas, y adaptar la gestión para mejorar la vitalidad, resiliencia y adaptación de las masas forestales a las futuras condiciones ambientales (Serrada Hierro et al., 2011; Sohn et al., 2012).

El objetivo general de la tesis es conocer el estado actual de los bosques españoles y aquellos factores climáticos e intrínsecos (densidad y estructura) que más están influyendo en ellos y establecer las medidas selvícolas más adecuadas que se puedan extraer de los resultados obtenidos. Para ello se ha muestreado en dos espacios naturales protegidos susceptibles de ser especialmente sensibles a los cambios que han ocurrido en las últimas décadas por la presencia de especies típicas de bosques templados que encuentran en la Península Ibérica su límite de distribución meridional: Parque Nacional de los Picos de Europa y el hayedo de Montejo de la Sierra declarado Sitio Natural de Interés Nacional y Patrimonio Natural de la Humanidad por la UNESCO. Entre los factores climáticos, se ha estudiado tanto la influencia de las variables climáticas (temperaturas y precipitaciones) sobre el

crecimiento y la dinámica forestal como el efecto de los eventos climáticos extremos como las sequías y las heladas tardías. En cuanto a los factores intrínsecos, se ha estudiado el efecto de la densidad sobre el crecimiento actual, la dinámica forestal y la competitividad de las especies.

1.5. Estructura y objetivos específicos

La tesis se ha organizado en ocho capítulos. El primer capítulo corresponde a la introducción general, donde se presentan los antecedentes y la justificación de los estudios realizados. Los siguientes cinco capítulos (capítulos 2-6) se corresponden a otros tantos estudios que ya están publicados. Estos capítulos reproducen los artículos en inglés tal y como están publicados, con las correspondientes secciones de introducción, material y métodos, resultados, discusión, conclusiones, agradecimientos y referencias. Además, se han incorporado los anexos al final de cada capítulo. Finalmente, en los capítulos 7 y 8, se presenta la discusión y conclusiones generales de la tesis.

Cada uno de los estudios tiene sus objetivos específicos:

i) En el capítulo 2 se estudia una masa mixta de haya (*Fagus sylvatica* L.), roble albar (*Quercus petraea* [Matt.] Liebl.) y abedul (*Betula pubescens* L.), situada al norte de la provincia de León y dentro del Parque Nacional de los Picos de Europa. Es una masa bien conservada donde no se ha producido ninguna corta durante el último siglo, lo que permite estudiar la dinámica natural de la masa a través del análisis de las liberaciones del crecimiento. Estas liberaciones son aumentos abruptos y sostenidos del crecimiento radial producidos por la muerte de árboles vecinos y la consiguiente reducción de competencia (Altman et al., 2014). Los objetivos son i) conocer la sensibilidad climática de las tres especies arbóreas, ii) analizar qué factores provocan e influyen en los sucesos de mortalidad y iii) analizar si dichas liberaciones van acompañadas de un aumento del establecimiento de plántulas.

ii) En el capítulo 3 se propone una nueva metodología para estudiar la evolución de la capacidad competitiva de las especies arbóreas en la misma masa que en el capítulo anterior a lo largo del tiempo. Los objetivos son i) estudiar la historia y la dinámica del bosque a través de las estructuras de edad y tamaño, ii) determinar los factores que influyeron en el crecimiento radial del haya y el roble albar y iii) analizar la influencia de los factores climáticos sobre la capacidad competitiva de ambas especies y su posible evolución futura.

iii) En el capítulo 4 se estudia El Hayedo de Montejo, un bosque mixto de haya, roble albar y rebollo (*Quercus pyrenaica* Willd.), con una larga historia de intervención antrópica que mantuvo una estructura de dehesa en gran parte de su superficie. Desde la década de 1960 los usos tradicionales (cortas y pastoreo) fueron prohibidos, lo que ha promovido la regeneración y densificación del bosque. Dada la posición del bosque, en el límite de distribución meridional y occidental del haya y el roble albar, se analiza el efecto del clima y del cambio de uso en la dinámica y la evolución de los crecimientos. Los objetivos de este capítulo son i) estudiar la evolución de la capacidad competitiva de las tres especies coexistentes y ii) analizar la importancia relativa del clima y la competencia en su crecimiento.

iv) En el capítulo 5 se estudia el efecto de la helada tardía ocurrida en 2017 en El Hayedo de Montejo. Este año hubo un invierno y primavera especialmente cálidos, lo que adelantó el inicio del periodo vegetativo. Tras el inicio de la brotación, se produjo una bajada de las temperaturas que alcanzó los -4,6 °C, dañando todos los brotes del año. El objetivo de este capítulo es analizar el efecto de la helada sobre el haya y el roble albar a distintas escalas, desde el nivel de órgano hasta el de bosque. A nivel de órgano, comparando los rasgos funcionales relacionados con el transporte de agua del árbol y el balance de carbono entre los árboles dañados y no dañados por la helada. A nivel de árbol, comparando el crecimiento radial de 2017 entre estos dos grupos de árboles. A nivel de rodal se analiza el impacto de las heladas primaverales sobre el índice de área foliar (LAI) y el índice de vegetación de diferencia normalizada (NDVI), distinguiendo entre

las zonas dominadas por haya y roble. A escala de bosque, se estudia el efecto de las heladas sobre el NDVI.

v) En el capítulo 6 se analizan las diferencias en el crecimiento y su resiliencia (Lloret et al., 2011) entre el haya, roble y rebollo durante las heladas tardías que ha habido en El Hayedo de Montejo en el último cuarto de siglo: 1995, 2010, 2013 y 2017. En este estudio se ha estudiado el impacto de las heladas y sus efectos en los años siguientes a nivel árbol y bosque, utilizando crecimientos radiales y series de NDVI, respectivamente. .

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CAPÍTULO 2. LONG-TERM IMPACTS OF DROUGHT ON GROWTH AND FOREST DYNAMICS IN A TEMPERATE BEECH-OAK-BIRCH FOREST

Este capítulo reproduce el texto del siguiente artículo ya publicado:

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Abstract

The role of climatic extremes on forest dynamics is still not fully understood. This is the case for droughts in temperate forests where growth of tree species is more driven by tree-to-tree competition than by climate. In this study we examine whether droughts shape growth trends and forest dynamics in a temperate forest of beech, oak and birch located in the "Picos de Europa" National Park in northern Spain. We used a dendroecological approach to quantify climate-growth associations and to evaluate growth resilience after droughts. We detected growth releases and quantified the increase in the number of trees established following each drought. Beech was the dominant tree species. Tree growth was only weakly related to climate variables in the three species studied. Oak was more resistant to drought than the other two species in terms of growth, with beech displaying higher vulnerability to drought. A significant association is displayed by all three species among droughts, growth releases and tree establishment pulses. After 1923 and following the dry 1940s, beech presented a peak of growth releases, whereas growth releases in oak and birch were concentrated in the 1960s and 1990s, respectively. Drought-induced growth releases probably reflect gap formation, these gaps being filled by recruitment of the three species.

2.1. Introduction

Droughts may trigger disturbances and drive forest dynamics (Shuman et al., 2009). Rapid climate change may increase the frequency of severe droughts, challenging the ability of tree species which usually have long lifespans and slow evolution rates, to locally adapt to the new climate conditions (Alberto et al., 2013). In drought-prone forests, climate is one of the main factors that determine their dynamics. Tree mortality caused by dry spells generates gaps and patches which are filled by tree regeneration during cool-wet periods (Villalba and Veblen, 1997). In this way, drought removes old or less vigorous individuals and favors the establishment of regeneration of the same tree species or even of different species with contrasting requirements (Brown and Wu, 2005).

In contrast, in temperate forests, tree mortality and gaps are often considered stochastic processes, not necessarily generated by climatic extremes such as droughts (McCarthy, 2001). Gap dynamics in these forests are characterized by small-scale disturbances in the mature forest canopy, where a single or a small group of trees dies, creating a "hole" in the canopy that is occupied by released regeneration (Runkle, 1985). Tree death can be related with multiple biotic (stem size, stand conditions, tree species and pathogens) and abiotic factors (storms, precipitation, topographic features, edaphic conditions and disturbance history) and is usually due to stem breakage or uprooting caused by wind-throw or standing death caused by root and butt diseases (McCarthy, 2001). The generation of gaps is a continuous process which may dominate the disturbance regime in these forests (Lewis and Lindgren, 2000). Furthermore, in contrast to drought-prone conifer forests, the impact of pests and fires on broadleaf temperate forests is typically limited and spatially heterogeneous, without large-scale dieback (Man, 2012; McEwan, et al., 2007; Parshall and Foster, 2002).

The influence of climatic extremes on temperate-forest dynamics is poorly understood due to the difficulty involved in separating anthropogenic or natural disturbance-induced successional changes from climate-related alterations (Prentice, 1992). Furthermore, in the case of temperate forests climate-growth associations are usually less relevant than in dry or cold forest biomes, and competition often becomes the most important driver of radial growth (Fernández-de-Uña et al., 2016; Lebourgeois et al., 2005; Sangüesa-Barreda et al., 2015). However, exceptionally dry years can lead to abrupt growth declines, even in temperate forests (Gazol et al., 2017; Stahle et al., 2000; Zang et al., 2014). Recent evidence indicates that droughts may be key to understanding the dynamics of humid broadleaf-dominated forests; synchronizing growth declines, large-scale disturbances and post-drought recruitment pulses (Pederson et al., 2014). In addition, growth decline and tree mortality in these temperate forests may be amplified under warmer and drier climate conditions (Bréda et al., 2006).

In Western Europe, mixed broadleaf forests dominate temperate oceanic regions which are predicted to experience more severe droughts and warmer

conditions during the 21st century (Jacob et al., 2014). Most importantly, the frequency and magnitude of extreme climatic events, such as dry spells, will also increase under predicted climatic scenarios (EEA, 2004). These extreme events are particularly important to understanding forest dynamics (Jentsch et al., 2007). Some of the temperate forests in Spain constitute the southernmost distribution limits of important tree species such as European beech (*Fagus sylvatica* L.) or the sessile oak (*Quercus petraea* Liebl.). These populations are situated in areas with a Mediterranean influence, characterized by warmer and drier conditions during the growing season, particularly in summer (Giorgi and Lionello, 2008). Therefore, droughts and warmer conditions may contribute to the substitution of the dominant tree species in these southern temperate forests.

In this study we reconstruct forest disturbances by studying the abrupt and sustained increase in radial growth in trees with improved growing conditions (e.g., more light availability) following the death of neighboring trees. This sudden increase in wood production corresponds to a growth release (Altman et al., 2014). We reconstruct radial growth dynamics and associated tree recruitment pulses in a temperate forest situated in the "Picos de Europa" National Park in Northern Spain, close to the limit of the southern range of European beech and sessile oak. No logging has taken place in this well-preserved forest over the past century, enabling us to characterize the effects of climate on growth and to infer past gap dynamics. We aim to answer the following questions: (i) what is the climatic sensitivity of the tree species? (ii) is climate the driver of growth releases in the study area and do these releases underlie an increase in tree establishment? (iii) what factors influence growth releases?

Since the species studied in this case are close to the limit of their southern range, we hypothesize that climate has an important influence on growth and that extreme climatic events drive the growth releases and the establishment of recruitment in this temperate forest.

2.2. Materials and methods

2.2.1. Study area

The study area comprises mixed, uneven-aged forest of European beech (*Fagus sylvatica* L., hereafter beech), sessile oak (*Quercus petraea* (Matt.) Liebl., hereafter oak) and birch (*Betula pubescens* Ehrh., hereafter birch). The three species are deciduous and form conspicuous growth rings. Oak forms ring-porous wood, but beech and birch form diffuse-porous wood. Birch is an early-successional, shade-intolerant species whereas European beech is a late-successional, shade-tolerant species and sessile oak has intermediate characteristics (Frelich et al., 2015). Where European beech and sessile oak coexist, beech displaces oak due to its greater competitiveness and higher canopy cover (von Lüpke, 1998; Petritan et al., 2013). The site is located in León (northwestern Spain) at one of the southernmost distribution limits of beech and oak in Europe (**Appendix A**). Beech is the most abundant and widespread species throughout the studied forest. Oaks are more sparsely distributed, whilst birch appears at higher altitudes and on peatlands. The study area has undergone little human disturbance over the last century apart from cattle grazing and firewood collection. No logging has taken place over this period. There is a temperate oceanic climate with average temperatures of 8º C and annual precipitation of 1250 mm (data from Riaño station, ©AEMET, 42º 58' N, 05º 01' W, 1048 m a.s.l.; located at 20 km from the study site; see **Fig. 2.1**). The soils are Mollic Leptosols (FAO, 2015).

2.2.2. Field sampling

We conducted a field survey consisting of 103 sampling points systematically distributed on a square grid of 250 m x 250 m, occupying an area of 800 ha between coordinates 43º 8' 59'' – 43º 10' 29'' N, 4º 58' 48'' – 5º 2' 40'' W. The altitude ranges from 900 to 1600 m a.s.l. with a mean elevation of the sampling of 1283 m. The sampling was carried out during 2014 and 2015. At each sampling point, a pair of stereoscopic hemispherical images was captured using ForeStereo (patent MU2005-01738 of the Spanish Forest Research Centre) to characterize the neighborhood and

estimate stand basal area, tree density and diameter at breast height (DBH_{stand}) (Herrera et al., 2009; Rodríguez-García et al., 2014; Sánchez-González et al., 2016). In addition, one dominant tree of each species was randomly selected at each sampling point and its diameter at breast height (DBH) was measured. Two cores were extracted using a Pressler increment borer at breast height. These cores were always extracted perpendicular to the maximum slope. In total we cored 92 beech trees, 34 oaks and 11 birches. Topographical variables (altitude, slope and aspect) for each point were obtained from a Digital Terrain Model (PNOA®, © Instituto Geográfico Nacional, Spain) with a spatial resolution of 25 m.

2.2.3. Climatic data

Due to the lack of long, complete series of local meteorological data from stations situated in the study area, we used monthly data for precipitation, mean temperature and cloud cover from the 0.5º-gridded Climatic Research Unit (CRU) dataset (Harris et al., 2014) for all the analyses. CRU climatic data are considered to be homogeneous and are available from 1900 onwards with the exception of cloud cover data, which is available from 1950 onwards. We obtained the CRU climatic data for the period 1900-2014 from the 0.5º grid with coordinates 42.5º-43.0º N and 5.0º-5.5º W.

In addition, we used the reconstructed spring precipitation data in Pauling et al. (2006) and the self-calibrating Palmer Drought Severity Index (scPDSI) of the Old World Drought Atlas (Cook et al., 2015). Monthly potential evapotranspiration (PET) was estimated empirically using the method described in Willmott et al. (1985) from CRU temperature data. To show the long-term climate trends we fitted piecewise regressions to the data using the *segmented* package (Muggeo, 2008) in R statistical software (R Core Team, 2016).

2.2.4. Dendrochronological analyses

Cores were mounted on wooden supports and carefully sanded until the tree rings were clearly visible. The ring widths were then measured to the nearest 0.01 mm using the semi-automatic Lintab device with the TSAP-Win software (Rinntech, Heidelberg, Germany). Tree rings were visually cross-dated and measured, and cross-dating was further verified using the COFECHA program (Holmes, 1997).

We calculated the mean growth series for each individual and species using the *dplR* package in R (Bunn et al., 2016). Subsequently, these growths were transformed into basal area increments (BAI) as this variable is preferable to tree-ring width data for analyzing growth trends (Biondi and Qeadan, 2008). The BAI was calculated as follows:

$$BAI = \pi(r_t^2 - r_{t-1}^2) \quad (1)$$

where r_t and $r_{t\text{-}1}$ are the stem radius at the end and the beginning of a given annual ring increment corresponding to rings formed in *t* and *t*-1 years, respectively.

The age was estimated for the sampled dominant trees according to Rozas (2003b). This method is explained in **Appendix B**.

2.2.5. Climate-growth relationships

To determine the main environmental drivers of tree growth, we first removed biological trends in growth by calculating the residual ring-width chronologies for each species using the *dplR* package in R (Bunn et al., 2016). We used a double detrending procedure to remove long-term growth trends. We fitted a negative exponential curve to raw ring-width data, and then fitted a 32-year long cubic smoothing spline. The autocorrelation of the resulting residuals was removed using first-order autoregressive models. Pearson correlation coefficients were then calculated between the residual chronologies (mean series of the residual ring-width indices calculated for each species) and monthly mean temperature and precipitation. Correlation coefficients

were calculated from October of the previous year to November of the growth year considering that: (i) climate during the previous year affects growth during the following year (Camarero et al., 2015; Rozas, 2001), and (ii) growth can occur until November (Pérez-de-Lis et al., 2017). We split the data into three sub-periods (1911–1944, 1945-1979 and 1980–2013) to analyze changes in the relationships between climate and ring-width indices over time separately. We chose these three sub-periods of similar length due to the contrasting climatic characteristics of each, according to previous studies carried out in the Iberian Peninsula (García-Cervigón et al., 2012; Herguido et al., 2016). We did not analyze the first period in the case of birch due to the abundance of missing rings in the 1940s. The evolution over time of the Pearson correlations calculated between climatic variables and residual chronologies was analyzed for the best-replicated period, 1950–2014, using 20-year moving averages. Given the potentially long growing season in the temperate study zone (Pérez-de-Lis et al., 2017), we grouped the monthly climatic data into seasons to better reflect the changes in the climate-growth relationships.

2.2.6. Impact of droughts on tree growth

Due to the lack of reliable climatic data before 1900, we analyzed the most important reductions in BAI during the 20th century. Negative pointer years were determined as those years in which at least 60% of the BAI series of one species showed a BAI decrease of at least 60% relative to the average BAI in the 4 preceding years (relative growth change method; Schweingruber et al., 1990). We used these percentages to find the years with the greatest decrease in growth.

To characterize the climatic conditions linked to those negative pointer years we calculated the ratio between the climate values of these years and the average values for the 1900-2014 period, using monthly and grouped CRU climatic data. We identified the greatest differences and, furthermore, calculated the monthly climate variables with significantly ($p < 0.05$) different means between negative pointer years and the rest of the years. As all variables are homoscedastic and as temperature shows normal distributions while precipitation does not, we used a *t*-test for independent

samples with temperature and Mann-Whitney *U* tests for precipitation data. We considered temperature and precipitation from October of the previous year up to November of the growth year.

To check the discriminatory power of climate variables to predict abrupt decreases in growth, we calculated a logistic model in which the predicted variable takes a value of 0 for the negative pointer years and 1 for the rest of the years. The predictor variables were standardized to facilitate the interpretation of the coefficients. The existence of multicollinearity among explanatory variables was evaluated and avoided by calculating the variance inflation factor (VIF) and removing variables with VIF > 10 (Dormann et al., 2013). We used the same variables as in the comparison of means and also tested different grouped variables such as mean temperatures from March to April (spring) and from October to November (late autumn).

The growth response to unfavorable years and the ability to recover pre-disturbance growth levels after the disturbance were estimated for the different increment series through the resistance (R_t) and resilience (R_s) indices (Lloret et al., 2011):

$$R_t = BAI_i / BAI_{i-4} \quad (2)$$

$$R_s = BAI_{i+4} / BAI_{i-4} \quad (3)$$

These indices were calculated from BAI data and 4-year long pre- (i-4) and post- (i+4) disturbance periods were used. To calculate pointer years and resilience indices we used the *pointRes* package in R (van der Maaten-Theunissen et al., 2015). To compare the indices between the three species we used the Kruskal-Wallis test with Bonferroni *post-hoc*.

2.2.7. Reconstructing forest growth dynamics

To reconstruct forest disturbances, growth releases were detected through a quantification study of abrupt growth increments using the *TRADER* package in R (Altman et al., 2014). For beech and oak we employed the method proposed by Splechtna et al., (2005), which reduces the numbers of false releases (Altman et al., 2014). This method comprises two steps. Firstly, the average radial growth over the preceding 10-year period and the average radial growth over the subsequent 10-year period are calculated for each year of the growth series of each tree and the percentage growth change is obtained (Nowacki and Abrams, 1997). A release candidate is only considered if the growth pulse exceeds a 50% growth change threshold. Secondly, the boundary-line method (Black and Abrams, 2003), which standardizes the percentage growth change, is applied to the release candidates to remove the influence of age, size and other variables on growth (Black and Abrams, 2004). We followed Black and Abrams (2003), who defined moderate and major releases as those falling within 20–49.9%, and 50–100% of the boundary-line, respectively. Since the boundary-line method requires a large data set for calculating the boundary function (Black et al., 2009), it was only calculated for beech. In the case of oak we used the function proposed by Altman et al. (2013) for this species. There is no boundary function available for birch, hence we used the percentage growth change directly (Nowacki and Abrams 1997) to define the growth releases, taking into account that these would be overestimated (Altman et al., 2014). The boundary-line functions used for beech and oak are shown in **Appendix C**.

To analyze the relationship between the pointer years and the growth releases, we applied the modification of Ripley's *K(t)* statistic (Ripley, 1976) for one-dimensional, bivariate data (see for instance Bigler et al. 2007). We transformed the $K(t)$ into the $L(t)$ function which does not show an increasing trend. This function is interpreted as positive associations (temporal coupling) between drought and growth release when the $L(t)$ values are positive. To assess the significance of the calculated $L(t)$ values confidence envelopes were constructed based on 999 simulations calculated using the "circular" method (Wiegand and Moloney, 2004). We calculated the $L(t)$ function for time lags varying from 0 to 14 years.

The dated tree ring width measurements were used to fit a diameter-age potential model per species and to estimate the age of the all trees retrieved from the ForeStereo data. Hurdle regression models, using the *pscl* package in R (Zeileis et al., 2008), were fitted for each species and pointer year to identify differences in the number of trees per 10 year age class (response variable) between those plots where growth release was detected during the 11 years following a pointer year in any of the species (predictor variable = 1) and plots with no growth release in the same pointer year (predictor variable = 0). The hurdle regression is a two-component model: a truncated count component is employed for positive counts, and a hurdle component models zero vs. larger counts. A negative binomial and a binomial distribution were employed for the count and hurdle components respectively.

The influence of topographical and tree factors over the intensity of the growth releases was also evaluated. This was done by calculating stepwise linear regressions between the response variables (the maximum value of the boundary-line, or the percentage growth change for birch, in the subsequent 10-years for each pointer year, BL_{max}) and the predictor variables (DBH and age of the cored tree when the drought occurred, altitude, aspect and slope). Response variables were normalized through the inverse transformation $1/(BL_{max}+1)$. We only calculated regressions for the pointer years followed by more pronounced growth releases for each species. We checked the model assumptions and the absence of multicollinearity.

2.3. Results

2.3.1. Climate trends and drought events

In our study area, local and CRU climate data showed a gradual increase in temperatures and potential evapotranspiration together with a decrease in precipitation over recent decades (**Fig. 2.1a**). Reconstructed climatic data indicate that the 1940s were dry years and drought frequency has increased since 1990 (**Figs. 2.1b, c**). In addition, the period from 1990 to 2013 was the driest since 1800.

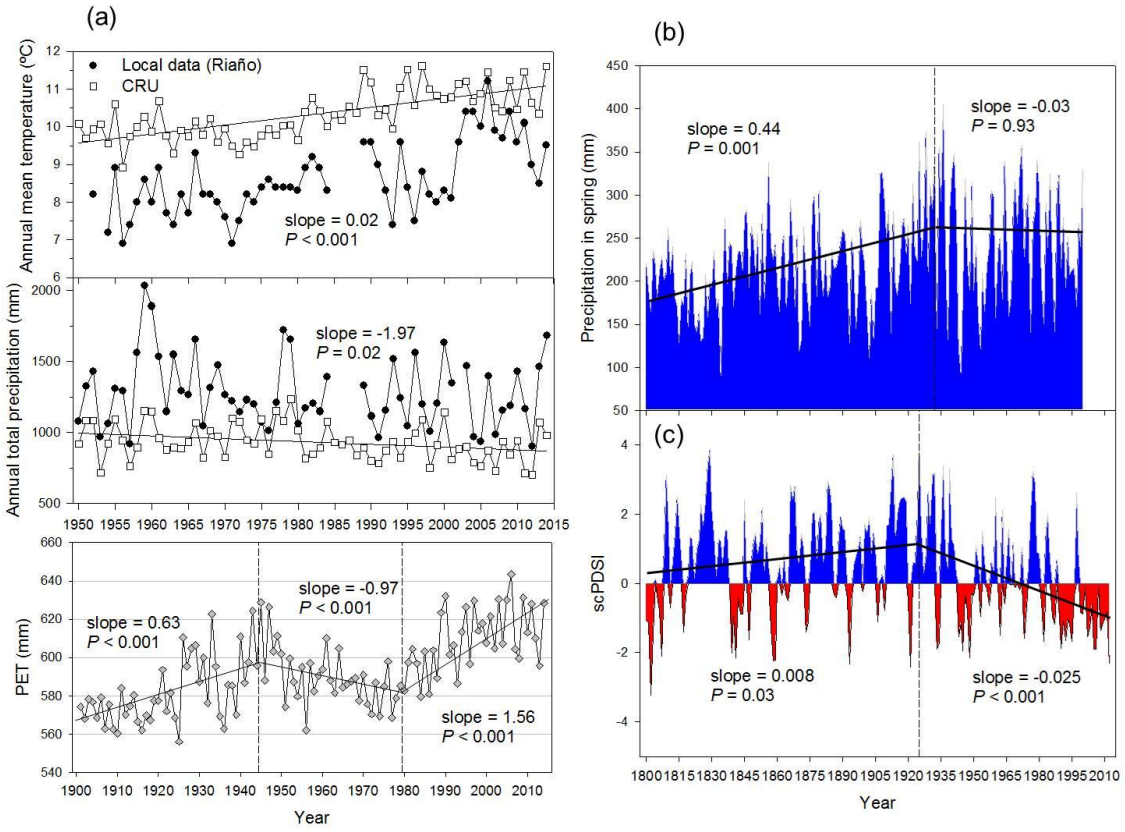

Figure 2.1. Climatic trends (annual mean temperature and total precipitation) and potential evapotranspiration (PET) in the study area (a) calculated using annual gridded (CRU data, empty symbols) and local climatic data (Riaño station, data with gaps). The coefficients of simple regressions fitted to CRU temperature and precipitation are shown. Reconstructed spring precipitation was taken from Pauling et al. (2006) (b) and the self-calibrating Palmer Drought Severity Index of the Old World Drought Atlas (Cook et al. 2015) (c) are also presented to highlight the 1940s dry period (positive and negative values of the scPDSI correspond to wet and dry periods, respectively). PET is calculated from February to November following Pérez-de-Lis et al. (2017). The slope of the simple and piecewise regressions fitted to CRU temperature and precipitation, PET, reconstructed spring precipitation and scPDSI charts are shown. Vertical dashed lines show the break points of the piecewise regressions.

2.3.2. Stand structure and growth sensitivity to climate

The sampled plots had an average basal area of 49.8 m^2 ha^{-1} and a mean density of 526 trees ha^{-1}. Beech, oak and birch were the more abundant species with mean basal areas (taking into account only those plots where the tree species appear) of 38, 25 and 21 m^2 ha^{-1} respectively (see **Table 2.D.1** in appendices). The cored oaks were

larger and older than the beeches or birches (**Table 2.1**). BAI was higher for oak than for the other two species (**Fig. 2.2**). The mean sensitivity of tree-ring width was lower in oak and higher in birch (see **Table 2.1**), whilst correlations of the individual growth series with the master series of each species were high for beech and birch, but low for oak, suggesting a higher growth coherence in beech than in oak. Abrupt BAI reductions in all species were noticeable in 1945 and 1995. Both birch and beech showed a high frequency of missing rings in the 1940s and 1990s indicating growth limiting conditions (**Appendix E**).

Table 2.1. Description of structural and dendrochronological variables of cored trees.

	Beech	**Oak**	**Birch**
Number of cored trees	92	34	11
Number of sampled cores	184	68	22
Mean diameter at breast height (cm)	38.0	61.9	27.1
Mean / maximum length of series (years)	119 / 314	153 / 441	106 / 200
Mean / maximum age (years)	141 / 342	197 / 487	130/218
Mean tree-ring width (mm)	1.28	1.30	0.70
Mean basal area increment (cm^2)	9.8	16.8	4.4
Mean correlation with master series	0.56	0.34	0.47
Mean sensitivity	0.37	0.28	0.49
Expressed Population Signal	0.94	0.69	0.68
Expressed Population Signal since 1900	0.98	0.85	0.79

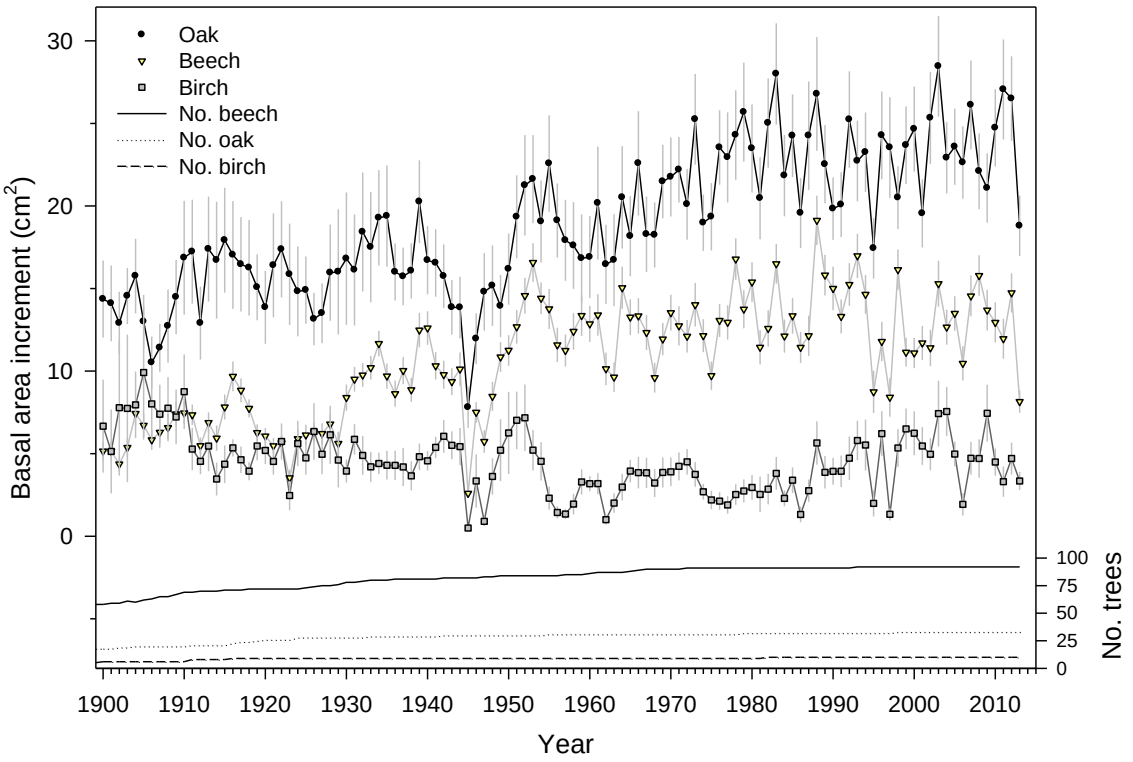

Figure 2.2. Growth trends (basal area increment, lines with symbols) for the three studied species (beech, oak and birch) since 1900 and number of cored trees (right y axis). Growth value area means ± SE. Different symbols and lines correspond to each species.

Tree growth was only weakly related to climate variables in the three species studied (**Fig. 2.3**). The correlations are in general low and not consistent across time periods. They only reach significance in a few instances. Climate-growth correlations were stronger in oak than in beech, particularly up to 1979, and very low in birch. In general, cool (and also wet in the case of oak) conditions from February to April and wet spring conditions enhanced growth in oak and beech. Birch growth displays a similar relationship with climate although correlations do not reach a level of significance in these periods.

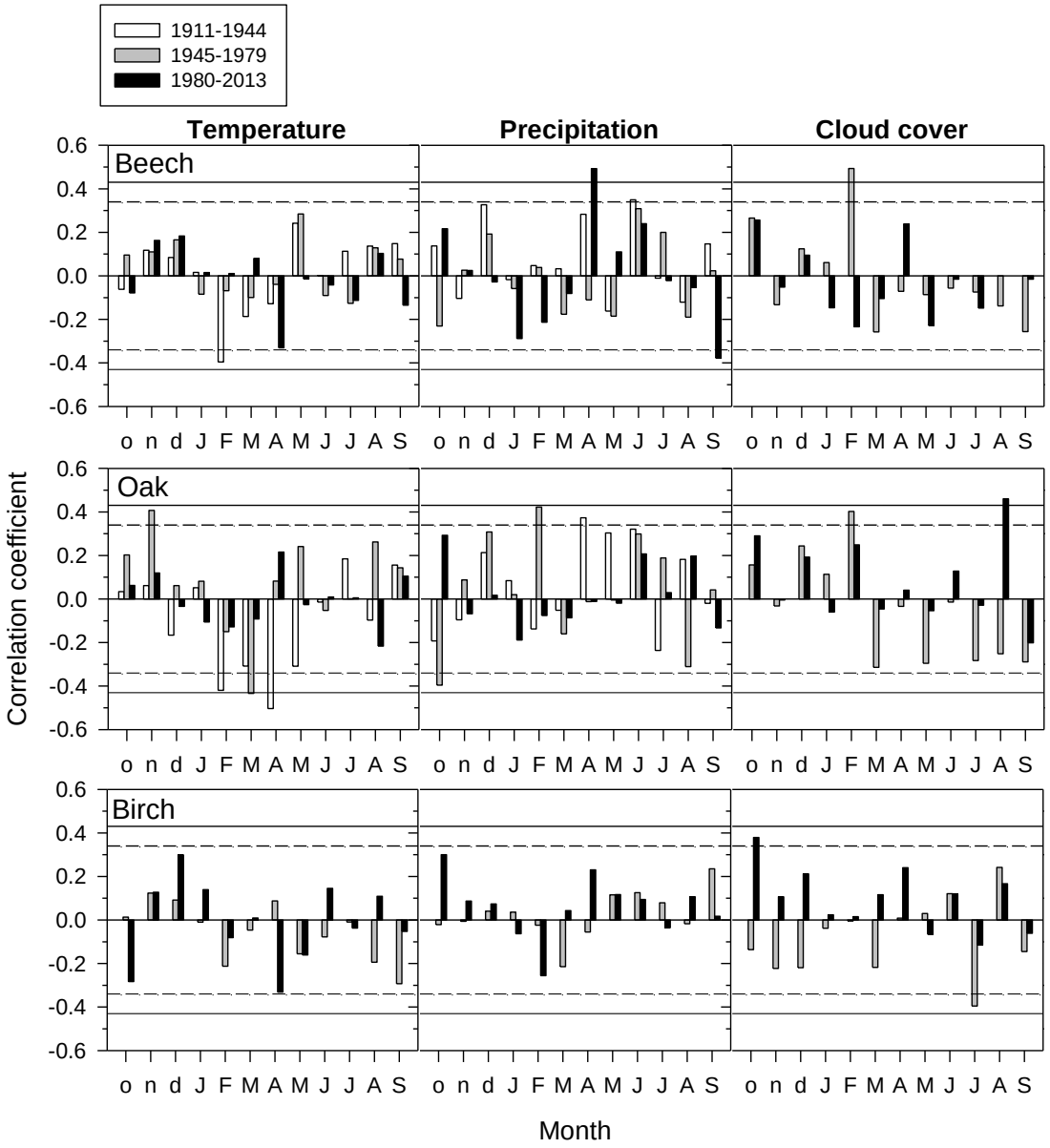

Figure 2.3. Climate-growth relationships based on Pearson coefficients, calculated by relating ring-width indices to monthly mean temperature, total precipitation and cloud cover. Correlations were calculated for three periods (1911-1944, white bars; 1945-1979, grey bars; 1980-2013, black bars) from the previous October through to November of the growth year considered (months with lowercase letters correspond to the previous year). Dashed and solid horizontal lines indicate significant correlations ($p < 0.05$ and $p < 0.01$, respectively).

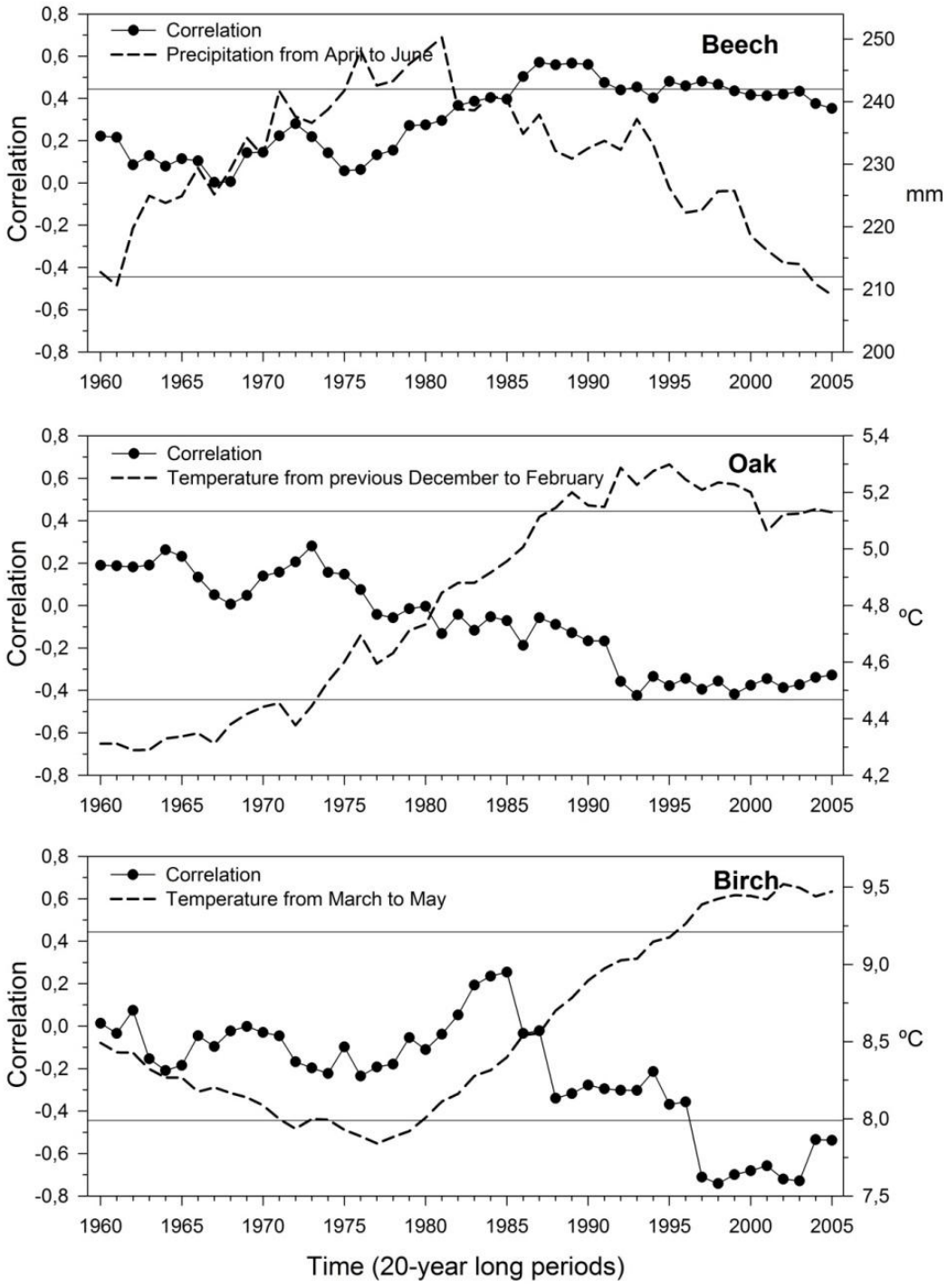

Figure 2.4. Moving averages of climate variables (dashed lines, right y axes) and moving climate-growth correlations (continuous lines with circles, left x axes) in beech, oak and birch. Pearson correlations were calculated for the 1950−2014 period using 20-year long intervals, relating ring-width indices and grouped monthly climate variables (mean temperature and total precipitation of grouped months). Significant (p < 0.05) climate-growth correlations are indicated by horizontal lines. Only the variables with the greatest changes over time are shown.

The warmer and drier conditions observed in the study area over the last half century corresponded to an increment in the negative associations between winter temperatures and oak growth and in the positive associations between growing-season precipitation (from April to June) and beech growth as conditions became drier, particularly from the 1980s onwards (**Figs. 2.1** and **2.4**). In the case of birch, associations between temperatures from March to May and growth became negative as climate warmed.

2.3.3. Climate extremes and negative pointer years

The negative pointer years were 1923, 1945 and 1995 in beech and 1923, 1945, 1947, 1962, 1995, 1997 and 2006 in birch, whereas no negative pointer years were observed in the case of oak. These years coincided with extreme climate events (see **Figs. 2.1** and **2.2**) and were characterized by warm spring-summer (March, April and July) and autumn (October and November) conditions and to a lesser degree, by low spring (April) precipitations (**Table 2.3**). The logistic model efficiently discriminated these negative pointer years with the exception of 1923 and 1962, which were characterized by cold early springs and unusually dry summers (**Table 2.2**). The accumulated precipitation from February to June in 1945 was half that of the long-term mean. In fact, the 1945 rings revealed the lowest average growth for the whole of the 20th century in the three species.

Table 2.2. Climatic characterization of negative pointer years observed in the three study species. Average values were calculated for the 1900-2014 period using CRU climatic data.

Year	Variable	Ratio (value /average value)
1923	Precipitation from previous October to previous December	0.6
	June precipitation	0.2
	April temperature	0.8
1945	Precipitation from February to June	0.5
	April temperature	1.4
1947	April precipitation	0.3
	July precipitation	0.3
	April temperature	1.3
1962	Precipitation from May to September	0.4
	March temperature	0.8
1995	Precipitation from March to April	0.4
	June precipitation	0.4
	Temperature from January to February	1.4
1997	Precipitation from February to April	0.2
	September precipitation	0.2
	Temperature from February to March	1.6
2006	Precipitation from May to June	0.5
	Temperature form October to November	1.3

Table 2.3. Variables with significantly ($p < 0.05$) different means between negative pointer years and the rest of the years (left) and slope coefficients of the logistic regression (right) relating pointer years to climate variables. P is precipitation and T is mean temperatures. The "•" symbol indicates interaction between considered variables.

Climate variables	*p*
P_{April}	0.04
T_{March}	0.04
T_{April}	0.001
T_{July}	0.03
$T_{October}$	0.001
$T_{November}$	0.05

Logistic model	Coefficients
Intercept	4.63
$T_{March-April}$	0.08
$T_{October-November}$	-0.68
$(T_{March-April})•(T_{October-November})$	-1.49

2.3.4. Growth responses to droughts

Extreme climate conditions were usually characterized by severe droughts, leading to a high abundance of missing rings in beech and birch (**Appendix E**). There were abundant missing rings in 1923, 1945, 1947, 1995, and 1997 and also, to a lesser degree, in 2006. In the case of beech, one third of the sampled trees lacked a complete ring in 1995 and 1997, and one fourth had missing rings in 1923 and 1945. In birch, the number of missing rings was greater, with more than 50% of the samples lacking a complete ring in 1947, 1995 and 2006, and all samples lacked the 1945 ring.

The three species showed similar responses for the selected negative pointer years considering the resistance and resilience indices (**Fig. 2.5**). Oak was the species least affected by droughts and showed significantly higher resistance indices than beech and birch ($p < 0.001$ in both). Birch showed the greatest growth reduction.

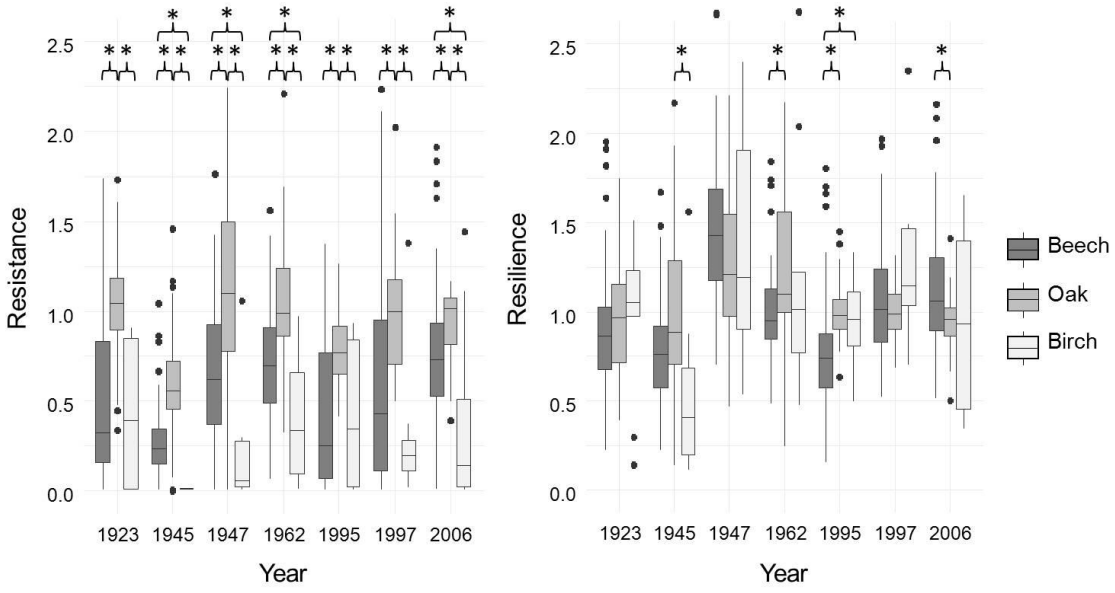

Figure 2.5. Resistance and resilience indices for oak (dark-grey box-plots), beech (grey box-plots) and birch (white box-plots) considering all the negative pointer years. Significant differences ($p < 0.05$) are marked with an asterisk.

2.3.5. Effects of drought events on forest dynamics

Most major releases in beech were observed in the late 1940s followed by the early 1930s, whilst in oak and birch releases were most frequent in the 1960s and 1990s, respectively (**Fig. 2.6**). After the 1995 and 1997 negative pointer years, the percentage of beech and oak trees showing releases was small when compared with previous droughts. The distribution of releases across the sampled plots was widespread and showed no spatial pattern (*results not shown*). In **Appendix F** we provide, as an illustrative example, a growth release over time of a selected beech after the 1945 severe drought.

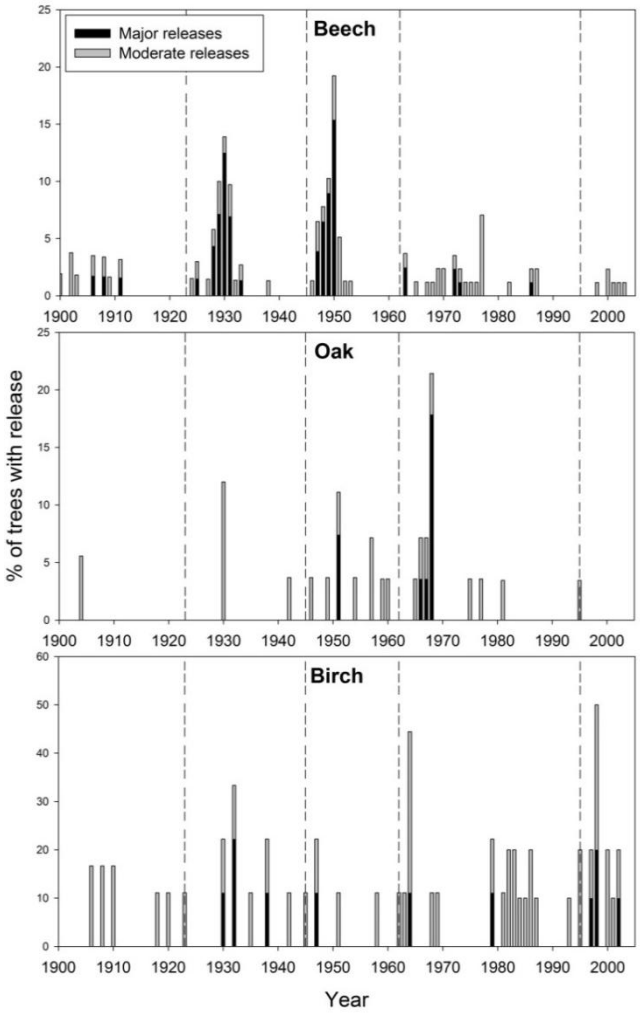

Figure 2.6. Major and moderate growth releases detected in beech, oak and birch during the 20th century. The negative pointer years 1923, 1945, 1962 and 1995 are highlighted with dashed vertical lines.

Pointer years related to droughts resulted in significantly ($p < 0.05$) increased growth releases 6-11 years, 7 years and 0-7 years later in beech, oak and birch, respectively (**Fig. 2.7**).

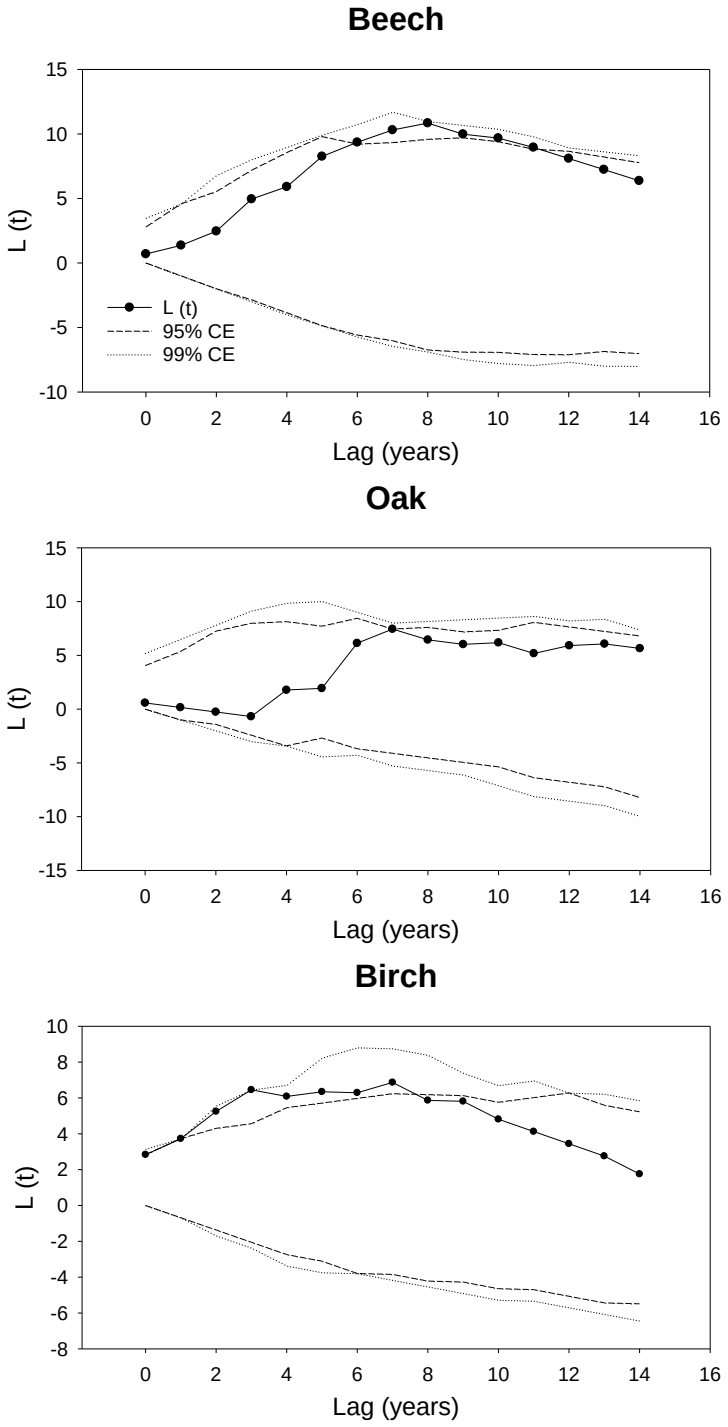

Figure 2.7. Bivariate event date analysis for growth release and drought. The *L(t)* function is shown for lags of 0 to 14 years. Dashed and dotted lines display the confidence envelopes (95% and 99% CE).

The analysis of the age distribution from the ForeStereo data shows a greater number of trees in age classes just established around the pointer years in the plots where growth releases were detected for the three species (**Fig. 2.8**). In the plots with growth release there are significantly more beeches and oaks established around the pointer years of 1923 and 1945/1947 and there are significantly more birches established around the pointer year of 1962. Due to the error in the age estimation we analyzed the differences in a window of 30 years, centered on the decade of each pointer year and considering years prior to the 1990s.

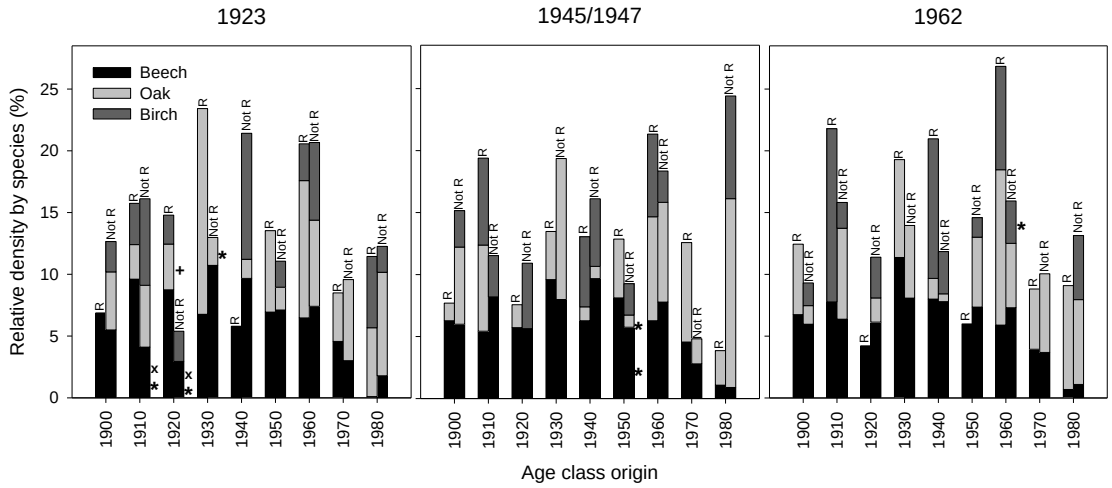

Figure 2.8. Relative density of the age class origin shown for each species, according to plots with growth release in each pointer year (R) and plots without growth release (Not R). The relative density (%) was calculated for each plot and species and then was averaged for the whole study area. Asterisks (*) indicates significant differences ($p < 0.05$) in the count component of the hurdle regression, symbols (^{X}) indicates significant differences ($p < 0.05$) in the hurdle component (zero vs. larger counts) and cresses (+) indicate differences that could not be analyzed with the model since all the values were zero in one of the groups.

Due to the inverse transformation of BL_{max}, the relationships between the maximum value of the boundary line and the coefficients in **Table 2.4** are reversed. We only performed regressions for the pointer years with the greatest growth releases for

each species, i.e. 1923 and 1945/1947 in beech, 1945/1947 and 1962 in oak and all pointer years in birch. No significant relationships were obtained for birch. One regression for each pointer year was calculated in beech due to the different relationships obtained in each one. According to the models, beech growth release increases with small diameter and younger age and in the case of the pointer year of 1923, growth release increases at high altitudes. Oak growth release increases with younger age and at lower altitudes.

Table 2.4. Regression coefficients (standard errors in parentheses) and adjusted R^2 for the linear models of the transformed maximum value of the boundary-line ($1/(BL_{max}+1)$) for beech and oak. Significance levels: * $p < 0.05$, ** $p < 0.01$ and *** $p < 0.001$, respectively. Variables were standardized prior to fitting the models.

	Beech		**Oak**
Pointer year	**1923**	**1945/47**	**1945/47 and 1962**
Intercept	0.782 (0.014) ***	0.803 (0.013) ***	0.835 (0.016) ***
DBH	0.031 (0.014) *	0.029 (0.014) *	
Altitude	-0.032 (0.014) *		0.049 (0.021) *
Age		0.037 (0.014) *	0.046 (0.021) *
Adjusted R^2	0.11	0.18	0.32

2.4. Discussion

The lack of recent, intensive silvicultural activity in the studied forest is corroborated by the mean ages of the dominant trees, which are 141 and 197 years old in the case of beech and oak, respectively, with a maximum age of 487 years (**Table 2.1**).

The correlations among individual ring-width series and the master series (**Table 2.1**) were within the range of values of the International Tree-Ring Data Bank (ITRDB) (Grissino-Mayer and Fritts, 1997) for beech. However oak and birch presented lower correlations with masters than at other ITRDB sites because many birches and aged oaks presented suppressed growth, with low variability between years and low sensitivity to climate (*results not shown*), possibly due to the competition from beeches, which display greater competitiveness (Manso et al., 2015).

The negative correlation between growth and temperature from February to April and the positive response to June precipitation (**Fig. 2.3**) have been observed in different beech populations of Circum-Mediterranean regions (Biondi, 1993; Gutiérrez, 1988; Piutti and Cescatti, 1997). This indicates a higher sensitivity of beech growth to water availability during the growing season at the study site in comparison to other European populations subjected to mild or cool conditions (Eckstein and Frisse, 1982; Lebourgeois et al., 2005; Rozas, 2001). In addition, warmer, drier conditions from the 1980s onwards were more detrimental to growth in the three species (**Figs. 2.1** and **2.4**). The sensitivity of oak to winter temperatures may be related to its higher proportion of living parenchyma in sapwood and higher respiration values during the dormant period compared with beech (Rodríguez-Calcerrada et al., 2015). Warmer winter conditions are associated with an increased consumption of non-structural carbohydrates, reducing the amount of reserves for starting growth the following year (Bréda et al., 2006). In any case, a markedly poor climatic signal in the tree growth series was observed (**Fig. 2.3**), even though the study populations were located near the southernmost limits of the species' distribution areas (**Appendix A**). Such a weak climatic signal indicates that climate conditions were not limiting to growth, as occurs in humid zones (Rozas, 2001) or cool, high-elevation sites (Camarero et al., 2015; Lebourgeois et al., 2005). Although mean climatic conditions are loosely associated with growth variability, extreme climate events such as severe droughts might trigger abrupt growth reductions and changes in forest dynamics (Martín-Benito and Pederson, 2015; Pederson et al., 2014).

It is possible that only extreme climate events, such as dry spells, reveal the growth sensitivity of temperate tree species to climatic constraints. In fact, the years with the lowest growth rates were characterized by warm spring and autumn conditions, but also by scarce precipitation during the growing season and the previous autumn and winter (**Table 2.2**) (see also Tessier et al., 1994). The synergistic effect of high temperatures and low precipitation prior to the start of the growing season can cause growth decline or even trigger tree death (Bréda et al., 2006). The years 1923 and 1962, which were not correctly classified by the logistic model (**Table 2.3**), had short vegetative periods caused by spring frosts and a dry summer. Indeed, the growth

releases in beech that occurred after 1923 were greater at higher altitudes (**Table 2.4**), where colder conditions prevail. Spring frosts combined with other stress factors such as drought, could lead to canopy dieback and increase mortality rates because frost fatigue (a decrease in cavitation resistance caused by freeze-thaw cycles) can predispose to xylem embolism and damage the expanding shoots and leaves (Hacke and Sauter, 1996; Thomas et al., 2002).

Oaks have higher resistance values compared to beeches, which in turn have higher values than birches (**Fig. 2.5**). Oak did not present missing rings, whereas missing rings were frequent in beech and birch (**Appendix E**). In addition, oak displayed higher resilience than beech and/or birch in 1945, 1962 and 1995, and oak was the only species to recover its previous growth after all negative pointer years ($R_s \geq 1$). This agrees with ecophysiological findings which show that beech is more vulnerable to drought than sessile oak when they coexist and are subjected to certain drought stress during the growing season (Aranda et al., 2000, 2005). In fact, a recent tree-ring study suggests that oak adapts better than beech to Mediterranean climatic conditions, characterized by dry summers (Dorado-Liñán et al., 2017). Birch was the species most negatively affected by drought, showing the greatest growth reductions although its resilience values were similar to those of beech.

In closed-canopy temperate forests, growth is often driven more by disturbances or biotic interactions (e.g., competition) than by climate (Cook, 1990; Fritts, 1962; Lebourgeois et al., 2005; Nowacki and Abrams, 1997). However angiosperms in temperate forests are vulnerable to hydraulic failure and tree mortality due to drought induced embolism (Choat et al., 2012). The warming-induced rise in tree respiration rates (Tjoelker et al., 2001), raising the consumption of carbohydrates and transpiration, could also increase the water requirements of these species making them more vulnerable to xylem embolism (McDowell et al., 2008). In our study, around 90% of the major releases detected took place during the ten years following each pointer year (taking into account all the pointer years for the three species: 1923, 1945, 1947, 1962, 1995, 1997 and 2006) (**Fig. 2.6**). There was a significant dependence between droughts and post-drought releases (**Fig. 2.7**), possibly caused by mortality of surrounding trees. As in other studies (Bigler et al., 2007), there were lags of 7 (for oak

and birch) to 11 (for beech) years between the detected disturbance (e.g., a drought) and a growth release. Droughts can cause tree mortality both directly and indirectly, predisposing trees to insect or pathogen attacks (Bréda et al., 2006). In the latter case, the tree may die a few years after the drought and this would trigger a lagged growth release in neighboring trees (Bigler et al., 2007). The impact of releases on annual growth differs according to the canopy position (Vašíčková et al., 2016), the species considered and their shade tolerance (Rozas, 2001). A high proportion of oaks are larger in size than the other species (see **Table 2.1** and **Appendix D**). This could have reduced the amount of detected releases because it is probable that they were already dominant trees during the analyzed periods and therefore less sensitive to additional canopy gaps than codominant or suppressed trees. However, previous studies also reported that mature dominant oaks tend to respond conservatively to canopy disturbances (Nowacki and Abrams, 1997; Petritan et al., 2017; Rozas, 2004), while beech shows a more pronounced response to disturbances (Peters and Poulson, 1994; Rozas, 2003a). The strongest release pulses took place after 1923 and 1945 in beech, after 1962 in oak and after 1995 in birch (**Fig. 2.6**). The largest growth releases were detected after the 1945 and subsequent droughts which characterized the dry period of the late 1940s (**Figs. 2.1** and **2.6**). This suggests that repeated drought may trigger growth releases due to tree mortality (McDowell et al., 2008; Pedersen, 1998; Villalba, 2002). Since 1980 there has been an increase in PET and temperatures and a decrease in precipitation (**Fig. 2.1**), with successive droughts affecting the study area. However, since 1990 few releases were identified in beech and oak, probably due to: (i) the maintenance of lower competition levels after the 1945 dry spell (reflected in the sustained growth increase in oak and beech; **Fig. 2.2**); and (ii) as trees grew and became dominant, growth responsiveness to disturbances was lost, depending on the shade tolerance of the species (Vašíčková et al., 2016). However, the increase in spring temperatures after the 1980s seems to have had an impact on birch growth (**Fig. 2.4**), which has shown an increasing rate of releases since 1990, although these results must be analyzed with caution given the absence of reference values for this species. The large percentage of birches with growth releases detected during that decade may be related to the use of the Nowacki and Abrams (1997) method without considering boundary-line standardization. In addition, the method used to detect releases does

not allow for assessment after 2003, so the effects of the 1995 and 1997 droughts on growth releases may not be fully uncovered.

Due to the different drought tolerance levels of beech, oak and birch, we expected that the growth releases would result from the mortality of the less drought-resistant beech and birch, thus benefitting oak. These releases seem to generate gaps of sufficient size to regenerate the three species (**Fig. 2.8**), not only the more shade-tolerant beech (Valladares et al., 2002).

Young or small oaks and beeches displayed greater growth increases after droughts (**Table 2.4**) due to their higher sensitivity to competition in comparison to older dominant trees (Schröder and Gadow, 1999; Maleki et al., 2015). The greater growth response of young and smaller trees to a decrease in competition allows the canopy ascension in these trees (Rentch et al., 2003). Altitude was found to have opposite effects on beech and oak growth. This might be explained by the fact that altitude is related to air temperature, with colder conditions at higher altitudes alleviating the negative effect of droughts on growth while also increasing the likelihood of spring frosts.

We expected a strong influence of climate on growth due to the location of the studied forest, close to the southern limit of the species distribution. However climate was not restrictive for growth, possibly because the mountainous relief creates favorable microclimate conditions and lessens the Mediterranean drought. In fact, the current distribution of beech in southern Europe does not match its climatic potential (Sánchez de Dios et al., 2016). Moreover, droughts become more limiting under high densities (Fernández-de-Uña et al., 2015) whereas our data indicate that moderate densities are maintained during the analyzed period, probably favored by cattle grazing. However, our results confirm that drought is the main driver of growth releases, adding further evidence of climate legacies in temperate forest dynamics (Pederson et al., 2014). Severe droughts, characterized by high temperatures and low precipitation during spring, summer and autumn, increase growth releases, possibly as a result of tree mortality. Mortality would lead to the formation of canopy gaps, generating conditions favorable for the establishment of the three species.

2.5. Conclusions

Our findings show that drought events influence growth and forest dynamics in a temperate, mixed forest. Severe droughts were key drivers of abrupt drops in tree growth during the 20th century. Beech and birch were the species which were most adversely affected by droughts in terms of growth loss, whereas oak was the most drought-resistant species. Droughts not only caused growth reductions, but were also linked to growth releases up to 11 years after drought occurrence. These releases are interpreted as reduced competition for resources due to increased tree mortality, which allows the establishment of recruitment of the three species.

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Appendix A

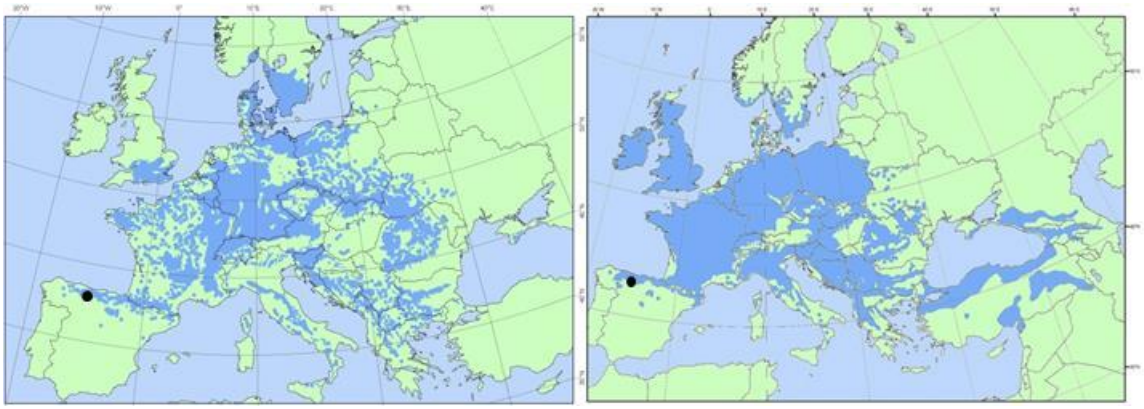

Figure 2.A.1. Distribution of *Quercus petraea* (left) and *Fagus sylvatica* (right) in Europe (EUFORGEN, 2009a, 2009b). Black dots show the site location in northwestern Spain.

References for appendix A

EUFORGEN, 2009a. Distribution map of Beech (*Fagus sylvatica*). http://www.euforgen.org/

EUFORGEN, 2009b. Distribution map of Sessile oak (*Quercus petraea*). http://www.euforgen.org/

Appendix B

Age at 1.3 m was estimated as follows. In those cases where cores reached the pith, age was estimated through cross-dating and counting of the rings. In all other cases, we first estimated the missing length to the pith and then the number of innermost lost rings. In these partial cores we used the arc of the innermost rings to estimate the length of the missing radius using a graphical method based on the convergence of xylem rays at the pith. In partial cores without conspicuous arcs, the length of the missing radius was estimated as the distance to the geometric center of the tree, assuming concentric growth. In the latter case, estimation was made by subtracting the corresponding cored length to the measured radius in the field, previously subtracting an estimated width of the bark. Bark thickness was estimated based on the tree diameter using equations from the Second Spanish National Forest Inventory (DGCONA, 1998). Functions used to estimate the bark thickness of beech and oak are as follows:

$$C_F = -0.00001d^2 + 0.0284d + 0.3545 \quad \text{(B.1)}$$

$$C_Q = 1.4407d^{0.4071} \quad \text{(B.2)}$$

where C_F is the bark thickness of beech, and C_Q is bark thickness of oak, and d are tree diameters measured at 1.3 m. Bark thickness of birch was also estimated with **B.1** function due to the lack of data for this species.

In partial cores, the number of missing rings was estimated using an empirical model of initial radial growth, a function of both the distance from the pith, and the mean radial growth rate of the 5 rings adjacent to the largest arc visible on the core (Rozas, 2003). We used these equations:

$$NMR_F = 3.41 - 3.15MRG5 + 2.07d - 0.037d^2 + 0.0002d^3 \quad \text{(B.3)}$$

$$NMR_Q = 3.37 - 2.26MRG5 + 1.22d - 0.022d^2 + 0.0001d^3 \quad \text{(B.4)}$$

where NMR_F is the number of missing rings in beech, NMR_Q is the number of missing rings in oak, and MRG5 is the mean growth rate of the innermost 5 rings of the core

and *d* is the tree diameter. The number of missing rings in birch was also estimated with **B.3** function due to the lack of a specific function.

References for appendix B

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Appendix C

The boundary-line function obtained for beech was the following:

$$y = -0.01825 + 5.28364e^{-0.83170x} \quad \text{(C.1)}$$

and the boundary-line function used for oak was (Altman *et al.*, 2013):

$$y = 5.0067e^{-0.664x} \quad \text{(C.2)}$$

where *x* are the 0.5 mm segments of growth (see Black and Abrams, 2004).

References for appendix C

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Appendix D

Table 2.D.1. Summary of the forest inventory carried out at the study sites. The results are the average for the plots where tree species appear. Values in parentheses are the standard deviation.

	Beech	**Oak**	**Birch**
No. plots	92	34	11
No. monospecific plots	62	8	0
No. mixed plots with beech	-	23	8
No. mixed plots with oak	23	-	4
No. mixed plots with birch	8	4	-
Basal area (m^2 ha^{-1})	38 (29)	25 (27)	21 (12)
Diameter at breast height, DBH (cm)	27.6 (9.4)	35.2 (23.6)	28.8 (12.0)
Density (No stems ha^{-1}, all stems)	460 (302)	193 (204)	339 (297)
Density (No stems ha^{-1}, stems with DBH < 32.5 cm)	286 (232)	81 (188)	228 (266)
Density (No stems ha^{-1}, stems with DBH > 32.5 cm)	141 (113)	87 (65)	111 (78)

Appendix E

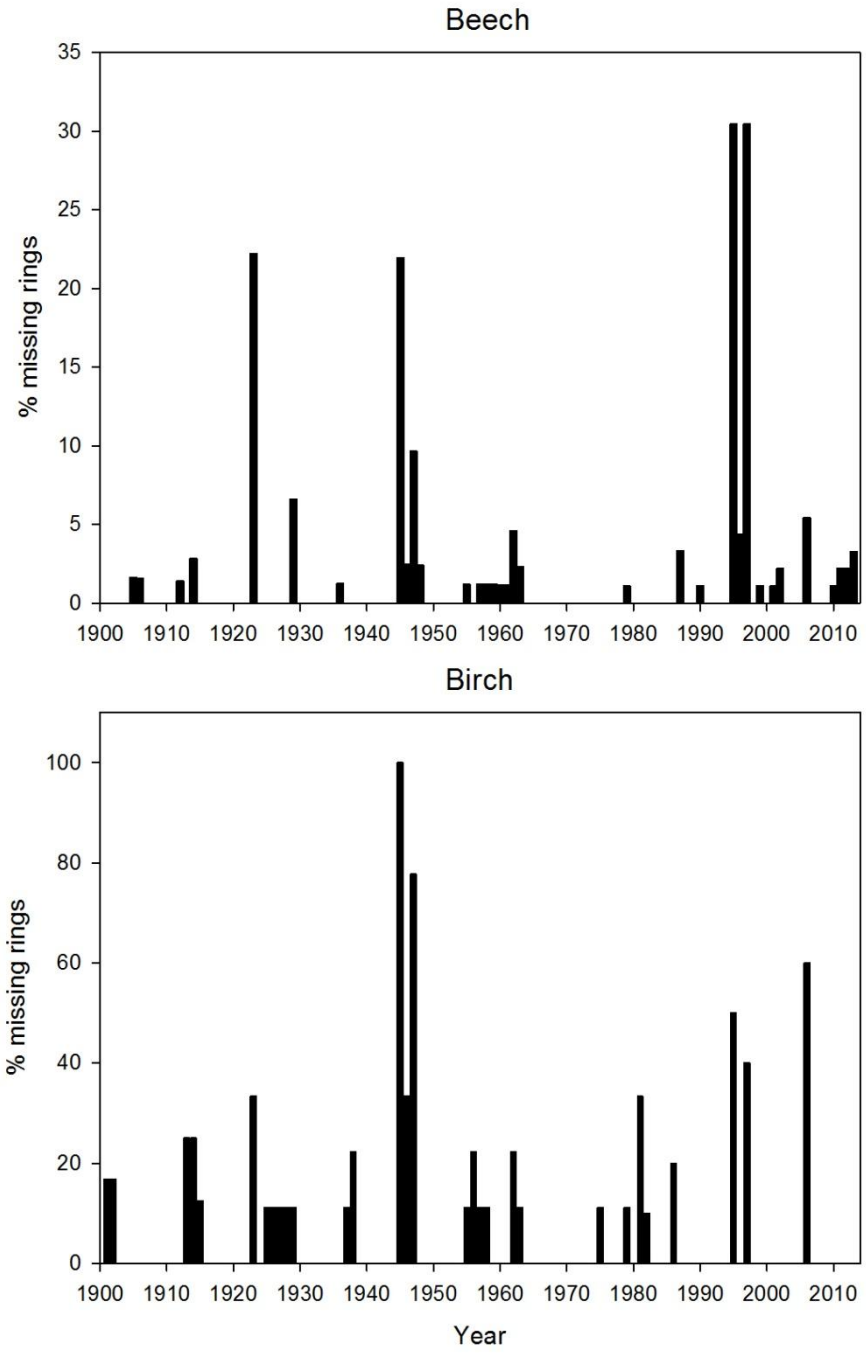

Figure 2.E.1. Missing rings observed in beech and birch tree-ring width series.

Appendix F

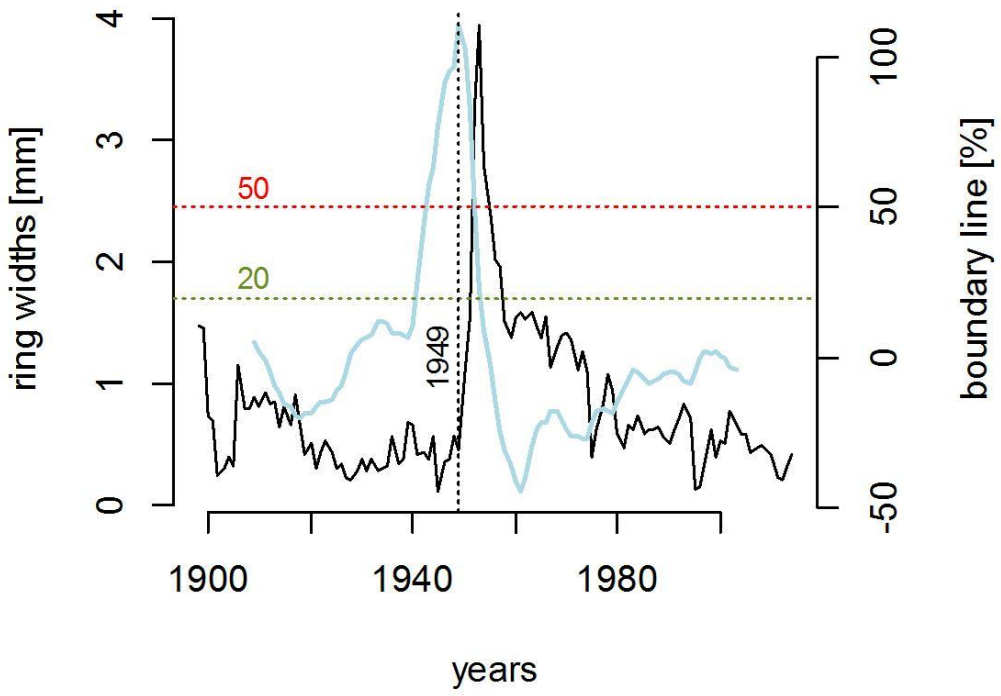

Figure 2.F.1. Notable growth release of a beech observed in 1949 and possibly connected to the 1945 drought and the release of light and nutrients due to mortality in the neighborhood of the tree. The black line shows the ring width and the blue line is the boundary line calculated according to Splechtna *et al.* (2005). According to the boundary-line method, positive growth changes between 20% and 49.9% (right *y* axis, dotted horizontal lines) are considered moderate releases, whereas growth changes above 50% are considered major releases.

References for appendix F

Splechtna, B.E., Gratzer, G., Black, B.A., 2005. Disturbance history of a European old-growth mixed-species forest – a spatial dendro-ecological analysis. J. Veg. Sci. 16, 511–522. https://doi.org/10.1111/j.1654-1103.2005.tb02391.x

CAPÍTULO 3. DROUGHT MODIFIES TREE COMPETITIVENESS IN AN OAK-BEECH TEMPERATE FOREST

Este capítulo reproduce el texto del siguiente artículo ya publicado:

Rubio-Cuadrado, Á., Camarero, J.J., del Río, M., Sánchez-González, M., Ruiz-Peinado, R., Bravo-Oviedo, A., Gil, L., Montes, F., 2018. Drought modifies tree competitiveness in an oak-beech temperate forest. For. Ecol. Manage. 429, 7–17. https://doi.org/10.1016/j.foreco.2018.06.035

Abstract

Over recent decades, forest management in Europe has increasingly moved towards the emulation of natural dynamics. Natural dynamics in beech-oak forests leads to the formation of monospecific beech stands, the oak usually being excluded or restricted to sites with poor growing conditions. However, beech is more vulnerable than oak to drought and high temperatures. In this study, we examine whether climate change could attenuate the dominance of beech and improve the competitive capacity of oak in an old-growth temperate forest located in the "Picos de Europa" National Park, northern Spain. We used a dendroecological approach to reconstruct the competitive capacity of beech and oak and developed a projection for the 21st century based on forecasted climate conditions under three different emission scenarios. Beech is the dominant tree species in the studied forest, where the disturbance regime has favored the replacement of oak by beech. In general oaks are older than beeches and most of the small trees are beeches. Our results show that this substitution process may weaken due to the vulnerability of beech to warmer and drier conditions. Climate change will benefit oak growth over beech over the course of the 21st century, as was observed in the late 20th century. However, the natural gap dynamic benefits beech due to its greater shade-tolerance. Therefore, if the resilience of the ecosystem is to be increased, management strategies favoring oak regeneration are necessary given the better adaptation of oak to climate change.

3.1. Introduction

Climate extremes such as droughts can reduce the productivity of temperate forests (Frelich *et al*., 2015) by leading to a decrease in radial growth or by triggering dieback episodes, often preceding mortality events or the replacement of one species by a more competitive or drought-tolerant tree species (Suárez *et al.*, 2004; van Mantgem *et al.*, 2009; Pederson *et al.*, 2014; Martin *et al.*, 2015; Sangüesa-Barreda *et al.*, 2015). Researchers and managers are interested in identifying and promoting mechanisms to enhance the resilience of these forests so as to make them less vulnerable to climate extremes such as severe droughts. Detailed studies of long-term relationships between

coexisting tree species may provide useful information to improve the resilience of such temperate forests under a scenario of regional warming and local drying.

Species mixing may improve resource use efficiency, tree growth and stand productivity due to niche complementarity and facilitation between coexisting tree species (Richards *et al.*, 2010). Several studies have shown that the negative effect of extreme drought on tree growth is often lower in mixed than in pure stands (Lebourgeois *et al.*, 2013; Pretzsch *et al.*, 2013; Mölder and Leuschner, 2014; Gazol and Camarero, 2016). However, this is not always the case (Grossiord *et al*., 2014; Forrester *et al*., 2016) and mixing may favor certain species more than others (González de Andres *et al*., 2017).

In recent decades, management of temperate beech-oak forests in Europe has moved towards emulating natural dynamics to increase the adaptability and resilience of these stands (Brang *et al.*, 2014). However, the dynamics in beech-oak forests often lead to the formation of monospecific beech stands, with oak usually being excluded or restricted to sites with poor growing conditions (Rozas, 2001b; Petritan *et al.*, 2017). Beech is more shade-tolerant, has a greater production of seeds (Harmer, 1994) and is more competitive than oak (Gazol and Ibáñez, 2010; del Río *et al.*, 2014), especially under gap-dominated disturbance regimes (Petritan *et al.*, 2013), which predominate in temperate forests (McCarthy, 2001). In addition, oak has difficulty regenerating (Pérez-Ramos, 2014) and as a result, a decline in the abundance of oak has been observed over recent decades in several European countries (Thomas *et al.*, 2002). However, beech is more vulnerable to drought (Aranda *et al.*, 2000, 2005; Piovesan *et al.*, 2008) and high temperatures than oak (Dorado-Liñán *et al.*, 2017). This greater vulnerability to drought could reverse the dominance of beech and increase the competitive capacity of oak in mixed beech-oak forests under warmer, drier climate conditions.

The competitive capacity of individual trees can vary considerably over time (Weber *et al.*, 2008; Sánchez-Salguero *et al*., 2015). In this study we use dendroecology to reconstruct the competitive capacity of beech (*Fagus sylvatica* L.; hereafter beech) and oak (*Quercus petraea* (Matt.) Liebl.; hereafter oak) in a mixed, old-growth

temperate forest located in the “Picos de Europa” National Park, northwestern Spain. We then develop a projection of this competitive capacity over the course of the 21st century based on the forecasted climate conditions under three different emission and climate scenarios (IPCC, 2014). The study area is located in the transition between the Mediterranean and the temperate bioregions and thus is subject to episodic summer droughts. We hypothesize that the forecasted rise in temperatures and decrease in precipitation will benefit oak growth over beech, attenuating the current greater competitiveness of beech. Our specific objectives are: (1) to study the forest history and dynamics through age and size structures; (2) to determine the factors that influenced radial growth in beech and oak; (3) to analyze the influence of climatic factors on the competitive capacity of beech and oak.

3.2. Materials and methods

3.2.1. Study area

The study site is located in the “Picos de Europa” National Park (Oseja de Sajambre, León, northwestern Spain). The climate is temperate oceanic with average temperatures of 8 ºC and annual precipitation of 1250 mm (data from Riaño station, AEMET, 42º 58’ N, 05º 01’ W, 1048 m a.s.l.; located at 20 km from the study site). The soils are Mollic Leptosols (FAO, 2015). This area represents one of the southernmost distribution limits of European beech and sessile oak in Western Europe (**Appendix**, **Fig. 3.A.1**). In the study area beech is the most abundant and widespread species throughout the studied forest (see **Table 3.1**), with a sparse presence of oaks. Both tree species are deciduous and form conspicuous annual rings. Oak forms ring-porous wood, whereas beech forms diffuse-porous wood. Natural dynamics prevail in this well-preserved forest situated in a protected area and no logging has taken place over the last century. Over this time the forest use has been limited to cattle grazing and occasional firewood extraction.

3.2.2. Field sampling

We performed the field survey during 2014 and 2015 consisting of 98 sampling plots systematically distributed on a square grid of 250 m x 250 m, occupying an area of 800 ha between coordinates 43º 08' 59'' – 43º 10' 29'' N, 4º 58' 48'' – 5º 02' 40'' W. The altitude ranges from 900 to 1600 m with a mean elevation of the sampling sites of 1283 m. In each plot a pair of stereoscopic hemispherical images was captured using ForeStereo to characterize the stand. The image segmentation and tree matching was carried out using the methods described in Sánchez-González *et al.* (2016). The matching process provides information on cross-sectional diameters along the detected stems, which are used to fit linear taper equations and individual tree diameter at breast height and volume (Rodríguez-García *et al.*, 2014). The instrument bias (non-detection due to image resolution) and occlusions effect is corrected, setting a maximum plot radius of 8 m to estimate stand basal area (BA), stand tree density (N), stand mean diameter at breast height (DBH_{stand}) and diametric distribution (Sánchez-González *et al.*, 2016). The ForeStereo estimates show high correlations with field measurements of BA and N in high forests without a shrub layer, as is the case of the studied forest, but show limitations in very dense forest with a large proportion of small sized trees or a dense shrub layer. In addition, a dominant tree of each species was randomly selected in each plot and its diameter at breast height (DBH_{cored}) was measured with a calliper. Two cores were extracted from the selected dominant trees using a Pressler increment borer at a height of 1.3 m and always perpendicular to the maximum slope. In total we sampled 90 beeches and 31 oaks. Topographical variables (altitude, slope and aspect) for each plot were obtained from a Digital Terrain Model with a spatial resolution of 25 m (PNOA, Instituto Geográfico Nacional, Spain).

3.2.3. Climate data

Due to the lack of long, complete series of data from meteorological stations situated in the study area, we used monthly data for precipitation and mean temperature from the 0.5º-gridded Climatic Research Unit (CRU) dataset (Harris *et al.*, 2014). CRU climate data are homogeneous and quality-controlled and data from 1901 onwards are

available. We obtained the CRU climate data for the period 1901-2013 from the 0.5º grid with coordinates 42.5º-43.0º N and 5.0º-5.5º W. Local (Riaño station, AEMET) and CRU climate data revealed an increase in temperatures, particularly from the 1990s onwards, together with a decrease in precipitation during the 20th century (**Appendix**, **Fig. 3.B.1**).

We considered the climate projections for monthly precipitation and mean temperature during the 21st century produced by the Coordinated Regional Climate Downscaling Experiment (CORDEX) (Jacob *et al.*, 2014) for the same 0.5º grid as that for which the CRU climate data was obtained. We considered three 'representative concentration pathways' (RCPs), which are climate projections consistent with a wide range of possible climate scenarios (0.3–4.8 °C global warming by the year 2099) according to anthropogenic greenhouse gas emissions (IPCC, 2014). We used data for the scenarios RCP 2.6, RCP 4.5 and RCP 8.5. The RCP 2.6 scenario represents a situation an increase in warming ranging between 0.3 and 1.7 °C during 21st century. Under the RCP 4.5 scenario temperature increases between 0.9 and 2.6 °C, whereas under the RCP 8.5 scenario warming ranges between 1.4 and 4.8 °C (van Vuuren *et al.*, 2011).

3.2.4. Dendrochronological data

Cores were mounted on wooden supports and carefully sanded until the tree rings were clearly visible. Tree rings were visually cross-dated. The ring widths were then measured to the nearest 0.01 mm using the semi-automatic Lintab device with the TSAP-Win software (Rinntech, Heidelberg, Germany). Cross-dating was further verified with the COFECHA program (Holmes, 1997).

We calculated mean growth series for each individual and these tree-ring widths were subsequently transformed into basal area increments (BAI) as this variable is better than tree-ring width for capturing growth trends (Biondi and Qeadan, 2008). The BAI was calculated as follows:

$$BAI = \pi(r_t^2 - r_{t-1}^2) \quad (1)$$

where r_t and r_{t-1} are the stem radial at the end and the beginning of a given annual ring increment corresponding to rings formed in *t* and *t*-1 years, respectively.

The age was estimated for the sampled dominant beech and oak trees in accordance with Rozas (2003), this method is further explained in **Appendix C**.

3.2.5. Stand structural features

To characterize the different structure types present in the studied zone, we first separated the data from the plots in which only beech was present from the data corresponding to the rest of plots. For each structure type, we then attempted to identify common patterns of diameter distribution using hierarchical Ward cluster analysis based on Euclidean distances (Ward, 1963). The input data for the analysis was the matrix of densities by diameter class, distinguishing between beech and oak. We used diameter classes of 10 cm from 7.5 cm (minimum measurement made by ForeStereo) to 57.5 cm. From 57.5 cm upwards we used a single diameter class due to the lower densities of trees of this size. We used Silhouette graphs to obtain the optimal number of clusters (Rousseeuw, 1987).

To infer the long-term canopy coverage patterns and to provide quantitative information on tree origin, the trees in which radial growth records reach the pith (37% of the sampled trees) were classified into two groups (Rentch *et al.*, 2003; Hart *et al.*, 2012): gap origin and understory origin. To classify the sampled trees into these groups, we compared the average radial growth for years 1 through 20 with the average growth for years 21 through 40 (McCarthy and Bailey, 1996). If the average for the first 20-year interval exceeded the average for the second 20-year interval, then the tree was classified as having originated in a forest canopy gap. If the average growth for the first 20-year interval was below that for the second 20-year interval, then the tree was classified as being of understory origin (Lorimer *et al.*, 1988; McCarthy and Bailey, 1996; Hart *et al.*, 2012). To confirm these quantitative classifications, the BAI data was graphically analyzed.

3.2.6. Factors influencing beech and oak growth

We used linear mixed-effects models to evaluate long-term BAI trends of beech and oak with the following variables as predictors or fixed factors: diameter at breast height of the cored tree in 2015 (DBH_{cored}, which represents tree size and growth potential); age of cored trees at the year of each annual radial growth (AGE) (which represents the growth trend with ageing); variables that characterize the physiographic variability within the study area: altitude, aspect, calculated as cosine of the maximum slope direction (1 indicates north, and 0 corresponds to south), and slope; structure type (from Ward cluster analysis); and variables characterizing the inter-annual climatic variability: annual mean temperature and total precipitation. To find the best model we tested different time intervals for the climate variables, although the maximum length of the interval was restricted from February to June, since this is the period when most radial growth occurs (cf. Pérez-de-Lis *et al.*, 2017). To test any CO_2-related fertilization effect we also included annual mean CO_2 values and annual mean rates of increase in CO_2 since 1959 as explanatory variables (data from Mauna Loa (Hawaii, USA) observatory ftp://aftp.cmdl.noaa.gov/products/trends/co2/). Only tree identity was considered as a random component of the models. Continuous variables were standardized. We only considered the 1959–2013 period because CO_2 data are only available for that period.

We adjusted a linear mixed-effects model with random intercept and fixed slope:

$$y_{ij} = \alpha + a_j + \beta z_{ij} + \varepsilon_{ij} \quad (2)$$

where y_{ij} represents log(BAI+1) for year i and tree j, α is the general intercept, a_j is the random intercept (tree identity), β is the vector of general slopes, z_{ij} is the vector of fixed effects and ε_{ij} is the error with a first-order temporal autocorrelation [AR(1)] structure. We used the log-transformation of BAI because it had a Gamma distribution. The distribution was tested using the Kolmogorov-Smirnov test.

To identify the best-supported model we constructed all possible combinations of alternative models from the full model considering main and random effects and the interactions between the fixed effects. As the restricted maximum likelihood method (REML) estimates an unbiased variance but does not allow models to be compared by minimizing the Akaike Information Criterion (AIC), we first adjusted all possible models using the Maximum Likelihood method (ML), then selected the best model by minimizing AIC and finally adjusted it again using the restricted maximum likelihood method (REML) (Zuur *et al.*, 2009). The existence of multicollinearity among explanatory variables was evaluated by calculating the variance inflation factor (VIF). VIF values greater than 10 mean that there is high collinearity among variables (Dormann *et al.*, 2013). The percentage of variance explained by the model was obtained in accordance with Nakagawa and Schielzeth (2013). These authors proposed a method adapted to mixed-effects models to estimate the total variance explained by the model (conditional pseudo-R^2) and the variance explained only by the fixed effects (marginal pseudo-R^2).

3.2.7. Retrospective analyses of species competitive dynamics

Using BAI data for the cored trees, we derived a retrospective competitive ability index of beech and oak over time. The index calculation was based on the assumption that for trees of the same species, higher BAI growth values imply higher competitive ability (Weber *et al.*, 2008). Trees from the same stand usually show a common climate signal in their tree-ring width series (Fritts, 2001) and differences in BAI patterns or trends are due to the distinct microclimates, distinct responses to the same climate and to the competitive stress with neighbors (Weber *et al.*, 2008). We were interested in extracting the specific (non-common) signals of growth patterns to analyze the differences in relation to climate. By sampling dominant trees it is possible to eliminate part of the growth signal due to competition with neighbors because of the asymmetric nature of competition (Schröder and von Gadow, 1999; Stadt *et al.*, 2007; del Río *et al.*, 2014; Maleki *et al.*, 2015) as well as to eliminate part of the noise produced by the disturbances of the forest dynamics (Vašíčková *et al.*, 2016).

The BAI patterns for beech and oak were compared by calculating interval trends (Schweingruber, 1988; Schweingruber *et al.*, 1990). An interval is a link between two adjacent years. An interval trend value shows the percentage of intervals with the same trend within a given period. In order to obtain this, firstly the BAI series of all beeches and oaks was smoothed, calculating it for 10-year moving intervals, since we are interested in the long-term BAI trends. Secondly, the number of ascending increments of BAI between consecutive years was summarized for each species. This was then transformed to percentages for species (i.e. percentage of beeches or oaks with ascending increments of BAI for each interval) to give a percentage series of competitive ability over time. To calculate the competitive advantage series of oak over beech (CA_{oak}), the percentage series of competitive ability for beech was subtracted from the percentage series of competitive ability for oak. In the resulting competitive advantage series, positive values indicate competitive advantage for oak, whereas negative values indicate competitive advantage for beech (Weber *et al.*, 2008). We reconstructed growth releases as a proxy of forest disturbances (this methodology is explained in **Appendix D**), and used only BAI data from the tenth year following the first release to avoid the inclusion of BAI data from when the cored trees had not yet reached the canopy.

We also constructed partial oak competitive advantage series using only the data from the clusters M2 and M3, but not from cluster M1 because of the small quantity and young age of the beeches. The Pearson correlations between CA_{oak} and the partial oak competitive advantage series were analyzed.

To reveal the relationships between climate and CA_{oak}, series were built for monthly temperature and precipitation, averaged in 10-year moving intervals. A regression was fitted between CA_{oak} (response variable) and the monthly series of climate variables (predictor variables) from October of the previous year to November of the growth year considering that: (i) climate during the previous year affects growth during the following year (Rozas, 2001a), and (ii) the growing season can last until November (Pérez-de-Lis *et al.*, 2017). Due to this potentially long growing season, we also grouped monthly climatic data into seasons to better reflect the relationships between competitive advantage and climate. The regression was fitted for the period

1901-2013 because climate data previous to this period is not available for this area. To identify the best-supported model we constructed all possible combinations and selected the model with the lowest AIC. The model assumptions were checked (normality, no multicollinearity and homoscedasticity).

3.2.8. Projecting competitive advantage of tree species as a function of climate forecasts

We projected CA_{oak} for the 21st century, using the previously mentioned regression model (in section 3.2.7). The predictor variable was the expected CORDEX values for the 21st century, according to the emission scenarios RCP 2.6, RCP 4.5 y RCP 8.5, smoothing it through 10-year-moving averages. The projected values of the competitive advantage for the year 2013 (first year of the series) were matched to the value of the previous retrospective analysis in this year. Finally a linear regression competitive advantage-year was fitted for each climate scenario.

3.3. Results

3.3.1. Characterization of the forest structure

We differentiated two clusters for pure beech plots: without abundant small sized trees (P1) and with abundance of small sized trees (P2). Three clusters were distinguished for the rest of the plots, which were mostly mixed stands: one with abundant small sized oaks (M1), another with abundant small sized beeches (M2) and one with scarce small sized oaks and beeches (M3) (see **Table 3.1** and **Fig. 3.1**). While young beeches are present in most of the forest, the presence of young oaks is restricted to those stands established after the 1940s (**Appendix**, **Fig. 3.E.1**). In all clusters with oaks, the age of the oaks is greater than that of the coexisting beeches (**Appendix, Fig. 3.F.1**). Considering all the clusters together; M1, M2 and M3, oak presented significantly greater (t = 3.01, P = 0.004) age (202 years on average) than beech (121 years).

The forest is uneven-aged, with an abundance of trees of all diameter classes (**Fig. 3.1**). Beech is the most abundant species (**Table 3.1** and **Appendix**, **Fig. 3.E.1**), but it is also the only species with a recent decrease in BAI for the period 1994-2013. In recent years, beeches have increased their growth in plots with abundant small sized oaks (cluster M1) but their growth has reduced in most of the rest of the studied area (**Table 3.1)**. Oak has retracted in the study area over the last few centuries, with only a scattering of trees remaining in the forest (**Appendix**, **Fig. 3.E.1**) and the only places where it is spreading are the abandoned lowland farming and grazing areas (the average altitudes for oak and beech in the studied area are 1161 and 1302 m, respectively). However, unlike beech, the BAI for oak shows no trend over recent years except in plots with abundant small sized beeches (cluster M2) (**Table 3.1)**. About 70% of cored trees of more than 200 years of age are oaks, with 342 and 487 years of age being the greatest ages observed for beech and oak, respectively.

Table 3.1. Summary of structure and growth data for beech and oak. Values are means (for basal area increment, BAI) and medians (for the rest of variables) with standard deviations in parentheses. Asterisks indicate significant differences (Wilcoxon's signed-rank test for paired samples) between both BAI periods considered. Significance levels: $*P < 0.05$, $**P < 0.01$ and $***P < 0.001$, respectively. Note that N, BA and DBH_{stand} are stand variables obtained from ForeStereo for all trees measured in the plot while DBH_{cored} is a variable of the cored trees.

Cluster	Species	No. plots	N (stems ha^{-1})	Basal area (m^2 ha^{-1})	DBH_{stand} (cm)	DBH_{cored} (cm)	BAI period 1974-1993 (cm^2 $year^{-1}$)	BAI period 1994-2013 (cm^2 $year^{-1}$)
P1	Beech	30	209 (103)	18 (21)	30 (11)	42 (16)	15.9 (12.2)	12.8 (11.6)***
P2		37	679 (267)	50 (19)	26 (4)	39 (8)	12.8 (8.9)	11.8 (9.9)***
M1	Beech	5	213 (90)	6 (7)	21 (7)	18 (6)	3.4 (2.8)	5.6 (3.8)***
	Oak	10	246 (163)	19 (9)	22 (14)	50 (14)	27.2 (9.3)	27.0 (11.1)
M2	Beech	9	488 (280)	36 (16)	25 (5)	34 (10)	7.2 (3.3)	6.3 (3.3)***
	Oak	9	104 (64)	19 (22)	56 (17)	57 (7)	12.6 (8.4)	13.7 (8.9)**
M3	Beech	9	159 (70)	9 (8)	30 (15)	40 (12)	17.8 (14.5)	18.1 (13.4)
	Oak	12	92 (50)	12 (22)	36 (27)	75 (18)	31.8 (16.9)	30.9 (15.3)
All	Beech	90	379 (334)	34 (23)	27 (9)	38 (13)	13.4 (10.9)	12.0 (10.8)***
	Oak	31	106 (135)	18 (20)	36 (23)	62 (18)	24.0 (15.2)	23.9 (14.4)

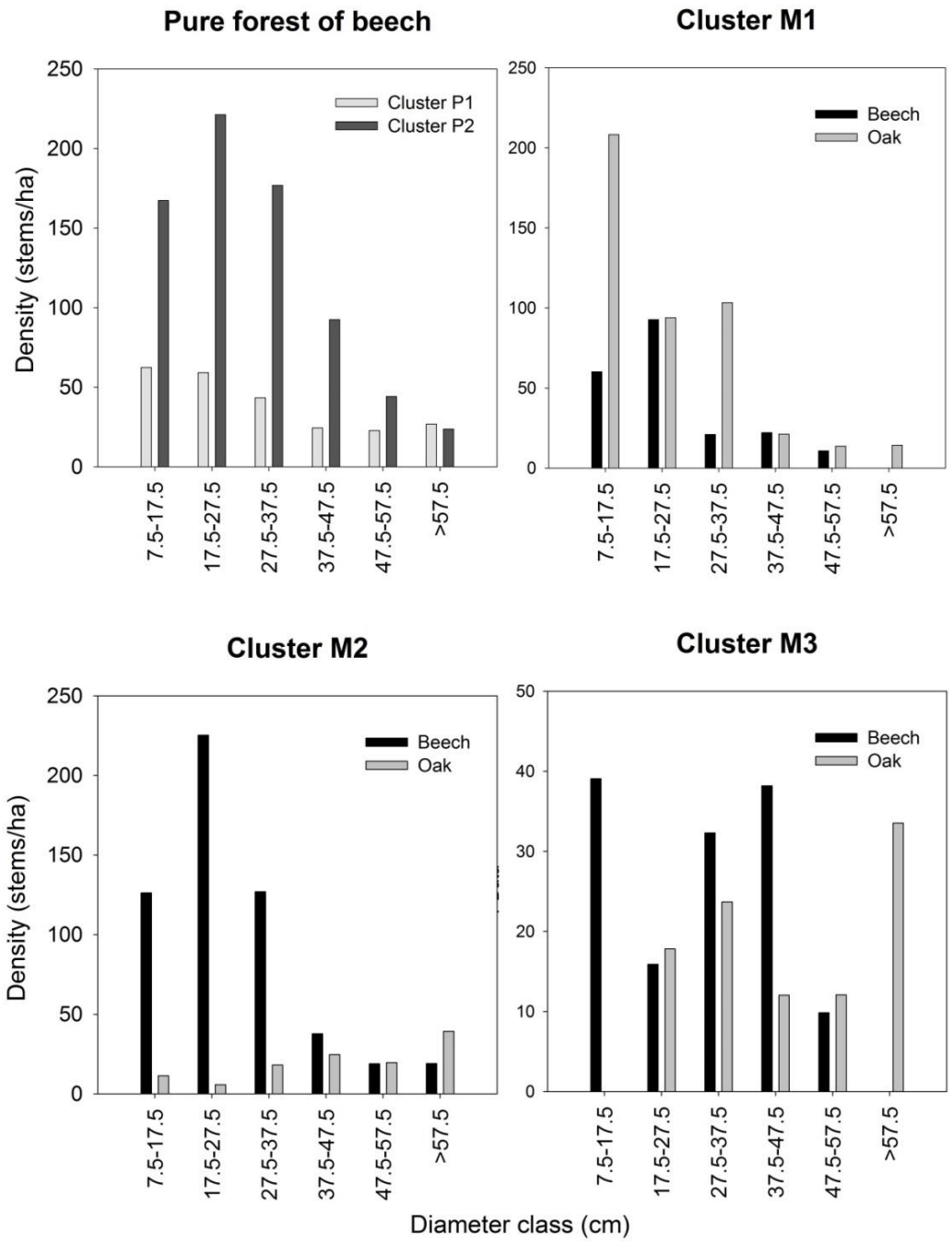

Figure 3.1. Size distribution (DBH_{stand}) of the clusters shown for the two studied species. Note that the y-axis scale varies between graphs.

The establishment of the currently dominant oaks occurred steadily over time whereas most of the dominant beeches date from between 1840 and 1880 (**Fig. 3.2**).

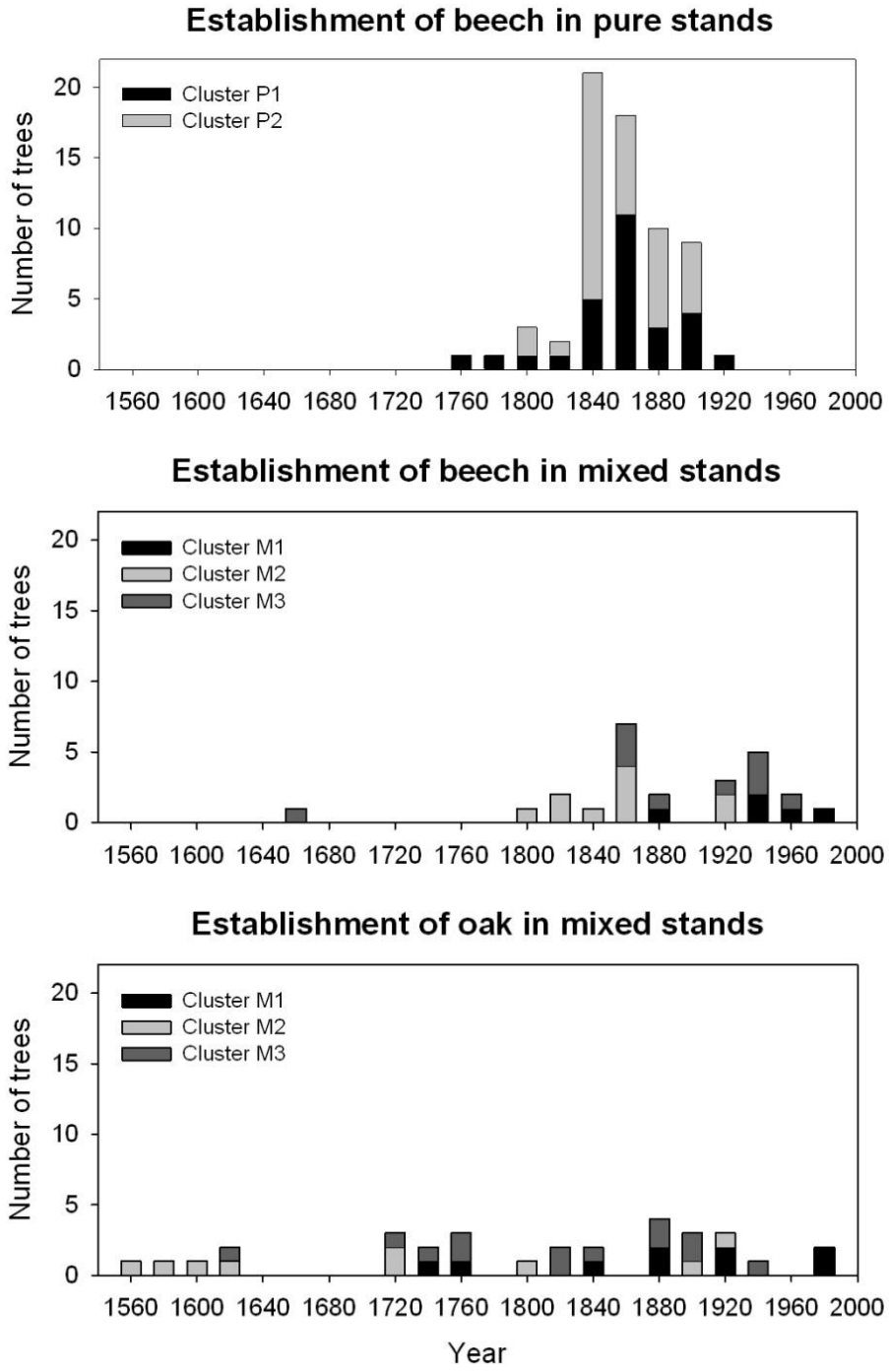

Figure 3.2. Establishment history of cored beeches and oaks (shown for 20-year age classes) presented according to size (DBH_{stand}) clusters.

Most of the dominant cored beeches (63%) were classified as being of understory origin (37% of gap origin) whereas most of the oaks (80%) were of gap origin (20% with understory origin). In the mixed stands the percentage of beeches with gap origin was higher (57%) than in pure stands (26%).

3.3.2. Factors influencing beech and oak growth

The coefficients of the variables of the most parsimonious BAI model for each species are shown in **Table 3.2**. The effects of the interactions are shown in **Fig. 3.3** and **3.4**. Taking into account the two selected models, the most important predictors of tree growth were: DBH_{cored}, AGE, annual mean rates of increase of CO_2, mean temperature from February to May, total precipitation from February to June, altitude and the interactions between the latter three variables. The most important variable of the beech growth model was DBH_{cored}, whereas in the oak model the most important predictors were DBH_{cored} and AGE, which produced opposite effects on BAI. Altitude was inversely related to the BAI of oak but its effect on beech growth is variable, depending on the climatic conditions (**Fig. 3.3** and **3.4**). Climatic variables are more important predictors of BAI in the case of beech than in oak. The CO_2 concentration was directly related to beech BAI. Temperatures seem to benefit growth whenever they are accompanied by wet conditions, whilst low levels of precipitation and warm temperatures associated with dry conditions lead to reduced growth. The percentage of BAI variance explained by the fixed and random effects (conditional pseudo-R^2) was 72% and 70% for the beech and oak model respectively, and the fixed effects explained (marginal pseudo-R^2) 62% and 58% of variance for the same species. In both models the VIF was lower than 3.

Table 3.2. Coefficients (standard errors in parentheses) for the best linear mixed-effects models of basal area increment for beech and oak, considering the 1959–2013 period. Significance levels: *$P < 0.05$, **$P < 0.01$ and ***$P < 0.001$, respectively. Predictors have been standardized previously to fit the models. Temperature is the average from February to May, and precipitation is the total rainfall from February to June. Carbon dioxide is the annual mean rates of increase in CO_2. "X" indicates interactions.

	Beech	Oak
Intercept	2.360^{***} (0.029)	2.981^{***} (0.045)
DBH_{cored}	0.589^{***} (0.028)	0.310^{***} (0.049)
AGE	-0.092^{***} (0.025)	-0.286^{***} (0.061)
Temperature	0.039^{***} (0.007)	0.038^{***} (0.007)
Precipitation	0.047^{***} (0.005)	0.014^{*} (0.006)
Altitude	-0.049 (0.032)	-0.173^{**} (0.059)
Carbon dioxide	0.042^{***} (0.006)	–
Temperature X Precipitation	0.123^{***} (0.005)	0.032^{***} (0.005)
Temperature X Altitude	-0.022^{***} (0.006)	–
Precipitation X Altitude	0.016^{**} (0.005)	-0.045^{***} (0.006)
Temperature X Precipitation X Altitude	0.044^{***} (0.005)	–

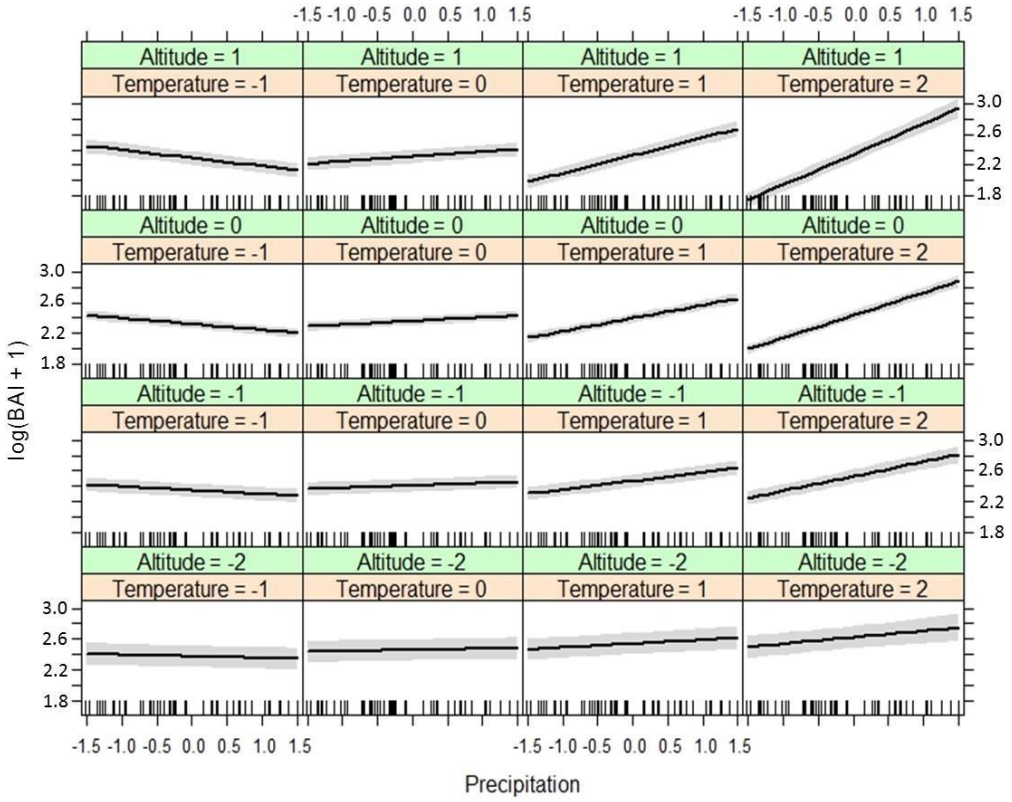

Figure 3.3. Effects of the interactions between climate variables and altitude on beech radial growth (log-transformed BAI data). The predictors are standardized. Temperature is the average from February to May, and precipitation is the total rainfall from February to June. Shaded bands indicate the confidence intervals. Positions of the data along *x* axis are denoted by tick marks.

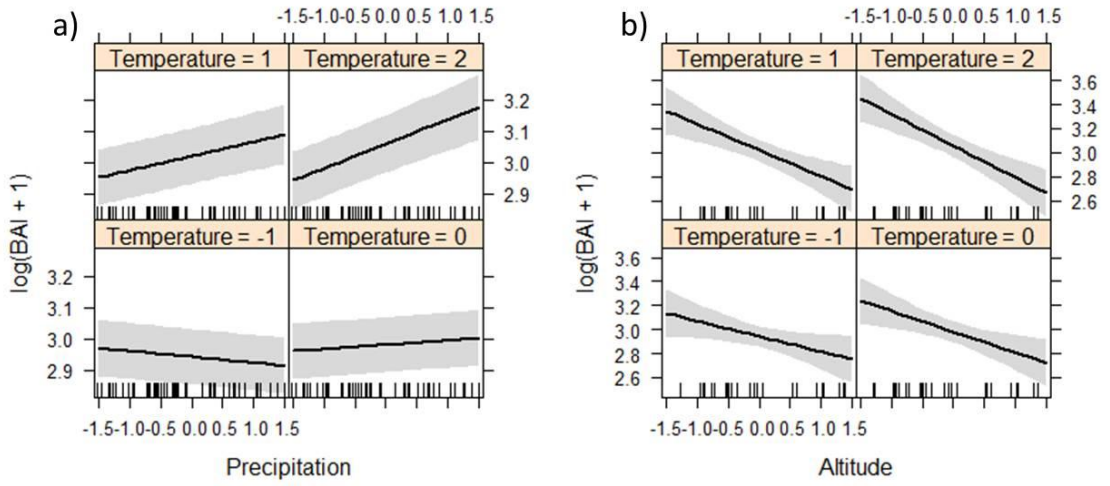

Figure 3.4. Effects of the interactions between temperature and precipitation (a) and between temperature and altitude (b) on oak radial growth (log-transformed BAI data). The predictors are standardized. Temperature is the average from February to May, and precipitation is the total rainfall from February to June. Shaded bands indicate the confidence intervals. Positions of the data along *x* axis are denoted by tick marks.

3.3.3. Retrospective analyses of species competitive dynamics

During the 20th century, there were alternating periods of competitive advantage for one or other of the two studied species (**Fig. 3.5**), with 46% of the years being favorable for oak growth and 54% of the years favorable for beech growth. From the 1960s onwards the percentage of years favorable for oak has risen to 64%. The Pearson correlations between CA_{oak} and the partial oak competitive advantage series for the clusters M2 and M3 were 0.793 ($P < 0.001$) and 0.565 ($P < 0.001$), respectively; thus, the general evolution of the competitive advantage is maintained in each cluster.

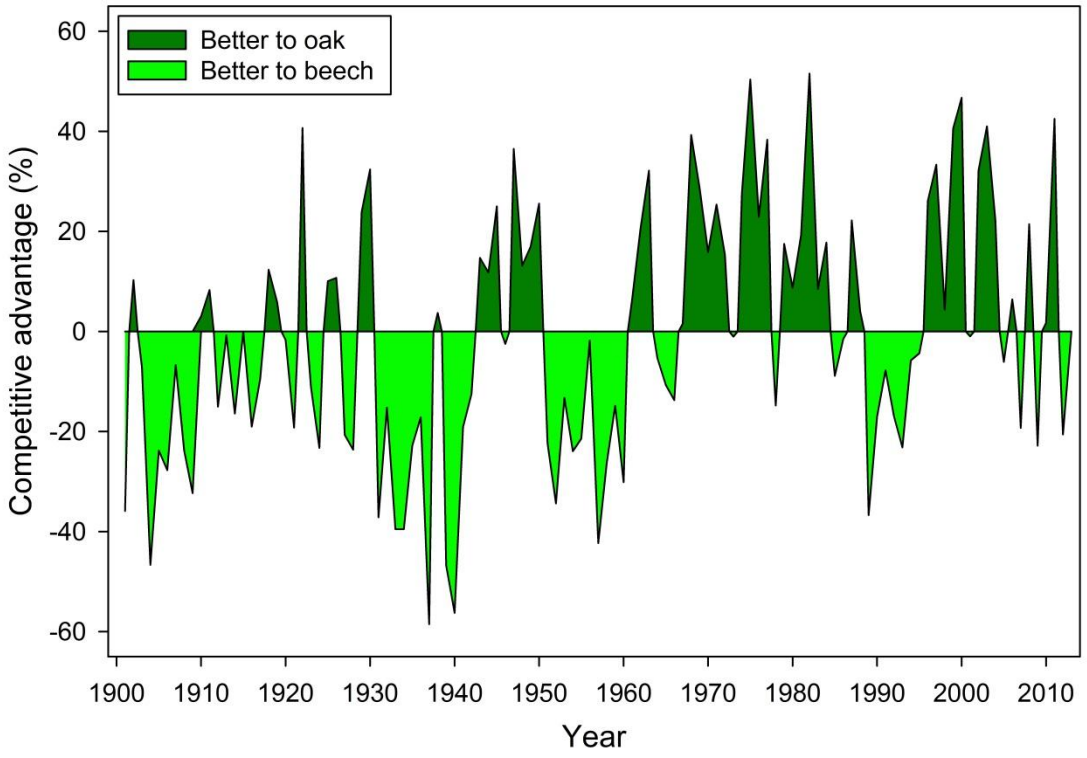

Figure 3.5. Reconstructed oak competitive advantage (CA_{oak}) from 1901 to 2013.

For the oak competitive advantage model (adjusted R^2 = 0.257), the variables selected are the temperatures of the winter previous to the growth period and late spring and summer precipitations of the growth period (**Table 3.3**). According to this model warmer winter temperatures and higher precipitations in August-September increase the competitive advantage of oak over beech, while wet conditions in June-July increase the competitive advantage of beech over oak. Although January and February temperatures are only marginally significant in the model, the Pearson correlation with CA_{oak} is significant (r = 0.299, P = 0.002).

Table 3.3. Regression calculated between the competitive advantage of oak and the climatic variables. VIF is the variance inflation factor.

	Coefficients	**Standardized coefficients**	***P***	**VIF**
Constant	-75.29		0.019	
Temperature $_{\text{January to February}}$	8.43	0.15	0.090	1.13
Precipitation $_{\text{June to July}}$	-0.29	-0.21	0.019	1.12
Precipitation $_{\text{August to September}}$	0.60	0.37	0.000	1.06

3.3.4. Projecting competitive ability of tree species as a function of climate forecasts

The projections forecast an increase in the competitive advantage of oak under the three emission scenarios (**Fig. 3.6**). According to these projections, oak will be favored by climate warming, although the slope of the regression line of each emission scenario is lower than 5% in two out of three cases. The rates of increase of the CA_{oak} for the twenty-first century are 17.3%, 4.7% and 1.6% for the RCP 2.6, RCP 4.5 and RCP 8.5 scenarios, respectively. The models showed R^2 of 0.58 (P <0.001), 0.16 (P <0.001) and 0.06 (P = 0.019), for the RCP 2.6, RCP 4.5 and RCP 8.5 scenarios, respectively. The low effect of the latter climate scenario on the CA_{oak} predictions is related to the trade-off between the rise in winter temperatures and the forecasted reduction in late spring and early summer precipitations, which would benefit oak, and to the reduction in August-September precipitations, which would benefit the competitive ability of beech.

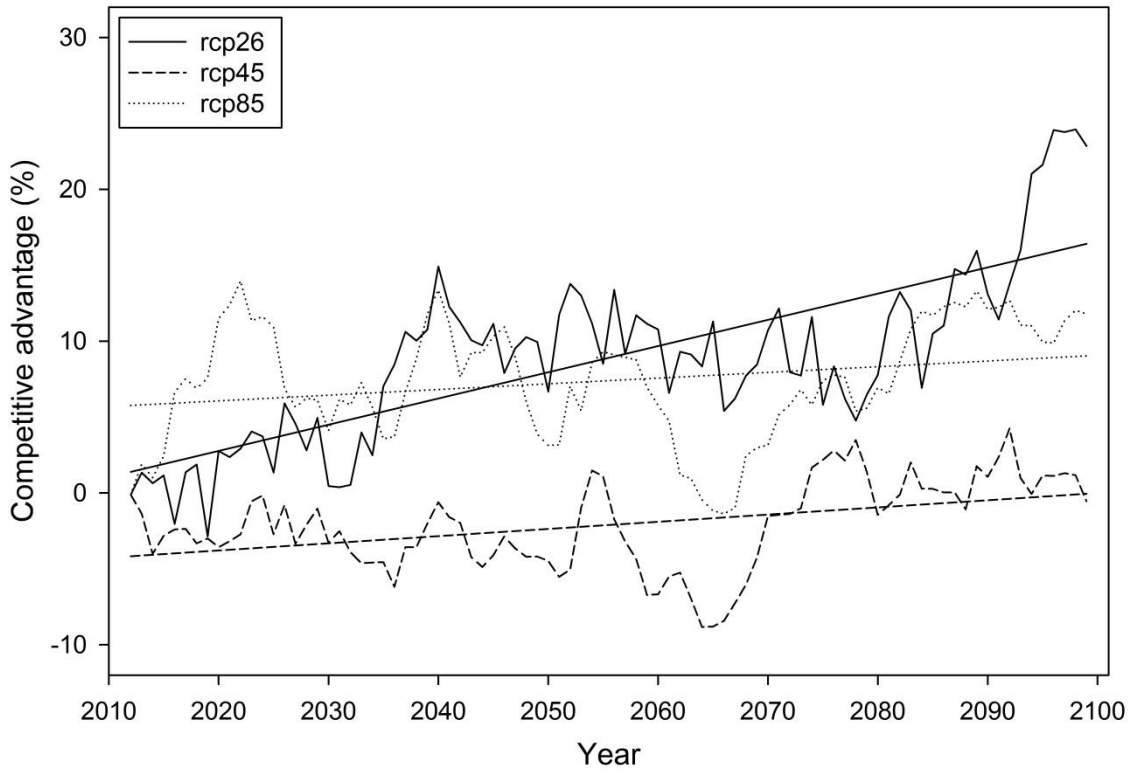

Figure 3.6. Projection of the competitive advantage of oak (CA_{oak}) over beech over the course of the 21st century for three emission and climatic scenarios (RCP 2.6, RCP 4.5 and RCP 8.5). Simple linear regressions were fitted for each scenario.

3.4. Discussion

3.4.1. Forest history and dynamics and growth trends

The dynamics in the studied mixed beech-oak forest, located at the south-western distribution limit of both species in Europe, is similar to other old-growth forests in other parts of the continent, in which the disturbance regime has favored the replacement of oak by beech (Rozas, 2001b; Rohner *et al.*, 2012; Petritan *et al.*, 2017). In general the oaks are older than beeches (**Fig. 3.2 and Appendix**, **Fig. 3.F.1**) and are heterogeneously distributed in form of scattered trees or forming small patches. The presence of young oaks is mainly circumscribed to the forest patches where trees established themselves after the 1940s (**Appendix**, **Fig. 3.E.1**). Conversely, beeches are spread throughout the area, forming mainly pure stands that comprise more than half of the study forest (**Table 3.1 and Appendix**, **Fig. 3.E.1**). The presence of young

beeches is common in most of the studied forest. In a great part of that forest, both tree species presented basal area values which are characteristic of old-growth forests (Hart *et al.*, 2012; Petritan *et al.*, 2015). Therefore the replacement of oak by beech has reached an advanced stage. However, this process of substitution may have taken place slowly. Beech has been both widespread and abundant in the region since at least 3000 cal. years BP (López-Merino *et al*., 2008) and in more recent times has been dominant over oak since the 19th century at least (Miñano y Bedoya, 1829; Engineers Corps, 1859). Most of the currently dominant beeches date from between 1840 and 1880 (**Fig. 3.2**). As in other mixed temperate Spanish forests (Gea-Izquierdo *et al.*, 2014; Dorado-Liñán *et al.*, 2017), during those decades there were social and economic changes that led to a reduction in grazing, and especially in transhumant cattle raising (García Sanz, 1978), which would have resulted in a reduction in logging intensity and an increase in regeneration in formerly grazed forests, such as the forest studied here (Miñano y Bedoya, 1829). The low proportion of beeches established before 1840 may be due to the lower sprouting capacity of beech in comparison to oak, which reduces the ability of the species to withstand grazing in the early stages of growth. The subsequent increase in the proportion of beeches also points to a small-gap disturbance regime typical of temperate forests (McCarthy, 2001). Small-gap dynamics may favor the establishment of a shade-tolerant species like beech (Niinemets and Valladares, 2006; Rozenbergar *et al.*, 2007), whereas the limited availability of radiation may hinder the regeneration of oak (Petritan *et al.*, 2013). Due to the reduction in logging intensity since the early 20th century, the natural dynamics of the forest would relegate the oaks to the areas in which the forest is expanding.

3.4.2. Factors influencing beech and oak growth

Growth (BAI) for beech and oak is mainly determined by tree size (DBH_{cored}), cambial age and the interactions between altitude, spring temperature and precipitation. As reported in previous studies (Cescatti and Piutti, 1998; Diaconu *et al*., 2015; Monserud and Sterba, 1996), most of the growth variance was explained by tree size (**Table 3.2**). AGE effect reflects the BAI decrease produced when trees enter the senescent phase

(Piovesan *et al.*, 2008; Kint *et al.*, 2012). Growth reached a peak when high temperatures and precipitations occurred simultaneously (**Fig. 3.3** and **3.4**). The overall positive effect of temperature on growth indicates that growth in the study area is limited by low temperatures, as occurs in some cold-temperate regions (Toïgo *et al.*, 2015; Lévesque *et al.*, 2016). However, in years with low spring precipitation, high temperatures may increase drought stress and hence decrease growth (Rozas, 2001a; Kint *et al.*, 2012). The growth of beech was also related to CO_2 values, indicating a potential fertilization effect, as occurs in areas where growth is limited by low temperatures (Keenan *et al.*, 2013; Camarero *et al.*, 2015; Madrigal *et al.*, 2015).

Beech showed a more pronounced sensitivity to climatic variables than oak, as observed in other studies (Kint *et al.*, 2012; Toïgo *et al.*, 2015; Dorado-Liñán *et al.*, 2017), which may indicate a better adaptation of oak to adverse climatic conditions including drought (Aranda *et al.*, 2000; Rubio-Cuadrado *et al.*, 2018).

3.4.3. Alternating beech-oak competitive ability dynamics

Growth trends may result from different interacting factors, abiotic factors such as climate and biotic factors such as tree age or social status, which operate at different spatial scales from patch to stand or biome, and also depend on forest management and disturbances (Dittmar *et al.*, 2003; Boisvenue and Running, 2006). We only used growth data from dominant trees, which are assumed to have been subjected to similar climate conditions and are less affected by forest dynamics.

Periods with a competitive advantage for one or other of the studied species alternate over the interval considered (**Fig. 3.5**). However, while years in which beech has a competitive advantage predominate in the first half of the 20th century, since the 1960s there has been an increase in the number of years in which oak has a competitive advantage. The growth series show a decline in beech but oak growth remains constant (**Table 3.1**). This different behavior of the two species is in accordance with the findings of other studies reporting a growth decline for beech since the 1960s associated with climate warming (Dittmar *et al.*, 2006; Piovesan *et al.*,

2008; Bontemps *et al.*, 2010; Braun *et al.*, 2010; Kint *et al.*, 2012; Dorado-Liñán *et al.*, 2017) and a growth increase for oak during the 20th century (Becker *et al.*, 1994; Bergès *et al.*, 2000; Kint *et al.*, 2012; Dorado-Liñán *et al.*, 2017).

High temperatures at the beginning of the year increase the competitive advantage of oak (**Table 3.3**). Oak produces earlywood prior to budburst whereas beech growth starts later; just after budburst with a maximal growth rate when the leaves are mature (Michelot *et al.*, 2012). Close to the study area, the radial growth of the oaks usually starts in February (Pérez-de-Lis *et al.*, 2017), while the beginning of the beech growth period varies from March to April (Čufar *et al.*, 2008; Martínez del Castillo *et al.*, 2016). In addition, we found a positive effect of temperature on oak growth (**Table 3.2**). Hence, a rise in temperature during the first months of the year could extend the growing period, thus increasing the growth rates of oak (Michelot *et al.*, 2012).

The competitive advantage of beech is directly related to precipitation in late spring and early summer. This agrees with observations in temperate European forests where beech growth is very sensitive to water-limitation and drought stress in the period between budburst and late July (Dittmar *et al.*, 2003; Piovesan *et al.*, 2008; Kint *et al.*, 2012) (see also **Table 3.2**). However, high precipitation in August and September improves the competitive advantage of oak, possibly due to the extension of the growth period, which can continue until late autumn (Pérez-de-Lis *et al.*, 2017). The higher sensitivity of beech to hydraulic failure (Aranda *et al.*, 2005) limits its growth in late summer and therefore this species probably benefits less from the rainfall that occurs at this time of the year in comparison to oak.

3.4.4. Projecting competitive ability of tree species as a function of climate forecasts

The three climate scenarios considered predicted an increase in temperatures and a decrease in rainfall. An increase in the winter temperatures and a reduction in June and July rainfall would give a competitive advantage to oak whereas a reduction in August and September precipitation would give a competitive advantage to beech

(**Table 3.3**). In the study area as in other mixed temperate forests (Kint *et al.*, 2012), these climate forecasts point to increasing competitive advantage for oak over the course of the 21st century (**Fig. 3.6**). However, warmer and drier scenarios were not associated with greater increases in the competitive advantage of oak due to the trade-off between climate variables. Our results only reflect growth projections, and other factors affecting forest dynamics (regeneration rates, tolerance to competition, mortality rates, disturbance regime) should also be taken into account in future research since these factors have an important influence on the persistence of coexisting tree species in temperate forests.

3.5. Conclusions and management implications

The replacement of oak by beech is a slow process due to the longevity of both tree species and their niche complementary under certain circumstances. Natural dynamics will restrict oaks to zones of forest expansion or to disturbance-related gaps in mixed forests, eliminating them from the rest of the forest patches dominated by the shade-tolerant beech. This process may be attenuated because of the vulnerability of beech to the forecasted warmer and drier conditions, which that would have a lesser effect on oak. In fact, according to our results, oaks have displayed greater adaptability than beech to the site conditions since the 1960s. In addition, the projected climate changes including warmer and drier conditions will benefit oak growth over beech over the course of the 21st century. Therefore, the ongoing retraction of oak may bring about a loss of ecosystem resilience due to the poorer adaptation of beech to warmer, drier conditions. The forecasted competitive advantage of oak will lead to the dominance of this species in scattered, favorable sites such as gaps, rocky outcrops or on the margin of beech-dominated patches. Management strategies aimed at maintaining a mixed stand with presence of both beech and oak should be considered as a means to better adapt to the forecasted climate change.

3.6. Acknowledgments

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Appendix A

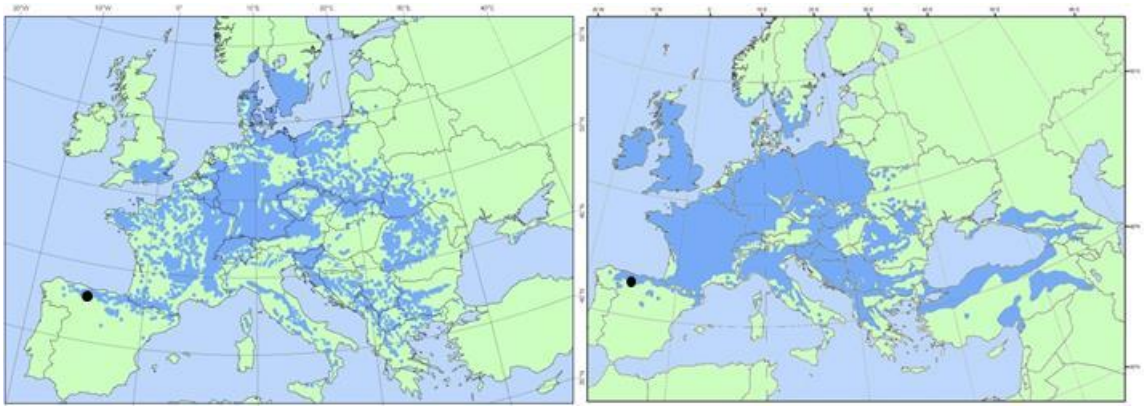

Figure 3.A.1. Distribution of *Quercus petraea* (left) and *Fagus sylvatica* (right) in Europe (EUFORGEN, 2009a, 2009b). Black points show the location of the study site in northwestern Spain.

References for appendix A

EUFORGEN (2009a). Distribution map of Beech (*Fagus sylvatica*). www.euforgen.org.

EUFORGEN (2009b). Distribution map of Sessile oak (*Quercus petraea*). www.euforgen.org.

Appendix B

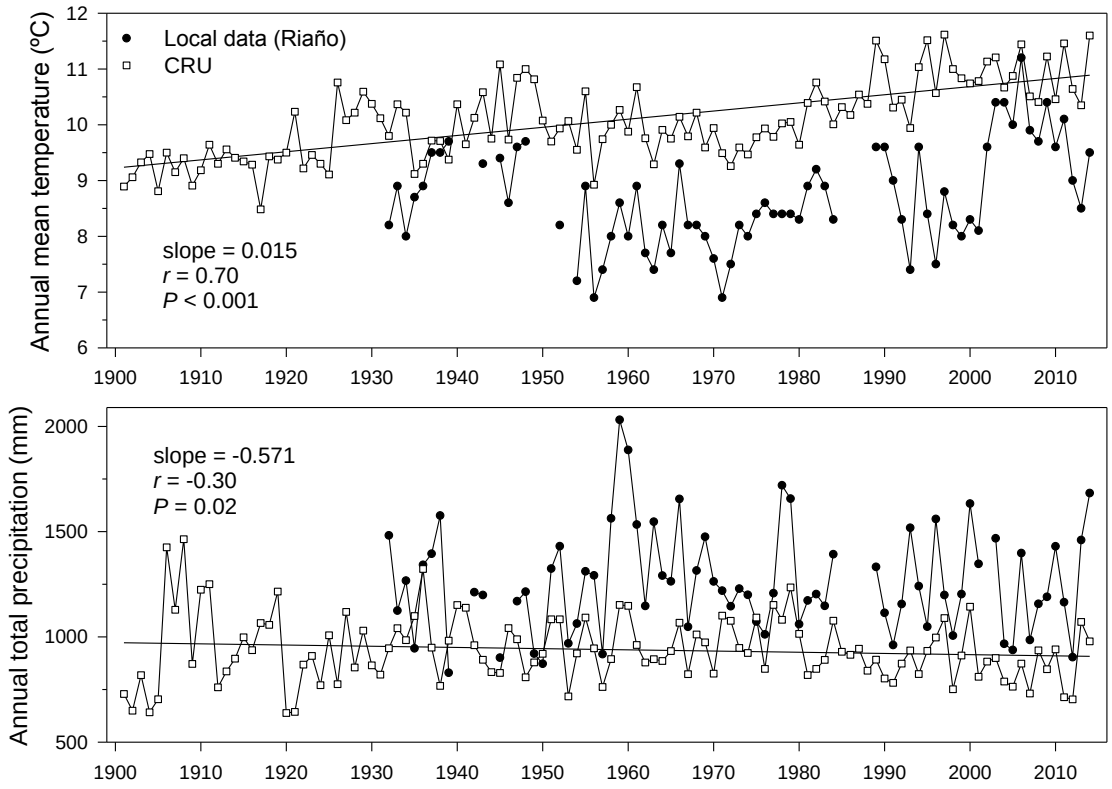

Figure 3.B.1. Climatic trends (annual mean temperature and precipitation) in the study area calculated using annual gridded (CRU data, empty symbols) and local climate data (Riaño station, AEMET, filled symbols, data with gaps). Simple regressions have been fitted in CRU temperature and precipitation. Pearson correlations between AEMET and CRU series were 0.62 ($P < 0.001$) and 0.49 ($P < 0.001$) for temperature and precipitation, respectively.

Appendix C

Tree age at 1.3 m was estimated as follows: In those cases where cores reached the pith, age estimation was performed through cross-dating of the rings. In the other cases, we first estimated the missing length to the pith and then the number of innermost lost rings. In these partial cores we used the arc of the innermost rings to estimate the length of the missing radius using a graphical method based on the convergence of xylem rays at the pith (Rozas, 2003). In partial cores without conspicuous arcs, the length of the missing radius was estimated as the distance to the geometric center of the tree, assuming concentric growth. In the latter case, estimation was carried out by subtracting the corresponding cored length to the measured radius in field, previously subtracting an estimated width of the bark. Bark thickness was estimated based on tree diameter using equations from the Second Spanish National Forest Inventory (DGCONA, 1998). Functions used to estimate the bark thickness of beech (C_F) and oak (C_Q) are:

$$C_F = -0.00001d^2 + 0.0284d + 0.3545 \quad \text{(C.1)}$$

$$C_Q = 1.4407d^{0.4071} \quad \text{(C.2)}$$

where d is tree diameter measured at 1.3 m.

In partial cores, the number of missing rings in beech (NMR_F) and oak (NMR_Q) was estimated using an empirical model of initial radial growth, a function of both the distance from the pith, and the mean radial growth rate of the 5 rings adjacent to the largest arc visible on the core (Rozas, 2003). We used these equations:

$$NMR_F = 3.41 - 3.15MRG5 + 2.07d - 0.037d^2 + 0.0002d^3 \quad \text{(C.3)}$$

$$NMR_Q = 3.37 - 2.26MRG5 + 1.22d - 0.022d^2 + 0.0001d^3 \quad \text{(C.4)}$$

where $MRG5$ is the mean growth rate of the innermost 5 rings of the core and d is the tree diameter at 1.3 m.

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Appendix D

To reconstruct forest disturbances, growth releases were detected through a quantification study of abrupt growth increments using the *TRADER* package in R (Altman *et al*., 2014). For beech and oak we employed the method proposed by Splechtna *et al*., (2005), which reduces the numbers of false releases (Altman *et al*., 2014). This method comprises two steps. Firstly, the average radial growth over the preceding 10-year period and the average radial growth over the subsequent 10-year period are calculated for each year of the growth series of each tree and the percentage growth change is obtained (Nowacki and Abrams, 1997). A release candidate is only considered if the growth pulse exceeds a 50% growth change threshold. Secondly, the boundary-line method (Black and Abrams, 2003), which standardizes the percentage growth change, is applied to the release candidates to remove the influence of age, size and other variables on growth (Black and Abrams, 2004). We followed Black and Abrams (2003), who defined moderate and major releases as those falling within 20–49.9%, and 50–100% of the boundary-line, respectively. Since the boundary-line method requires a large data set for calculating the boundary function (Black *et al*., 2009), it was only calculated for beech. In the case of oak we used the boundary function proposed by Altman *et al*. (2013) for this species.

The boundary-line function obtained for beech was the following:

$$y = -0.01825 + 5.28364e^{-0.83170x} \quad \text{(D.1)}$$

and the boundary-line function used for oak was (Altman *et al*., 2013):

$$y = 5.0067e^{-0.664x} \quad \text{(D.2)}$$

where *x* are the 0.5 mm segments of growth (Black *et al*., 2004).

For more information on release structures and the past disturbance regime of the studied forest see Rubio-Cuadrado *et al.* (2018).

References for appendix C

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Appendix E

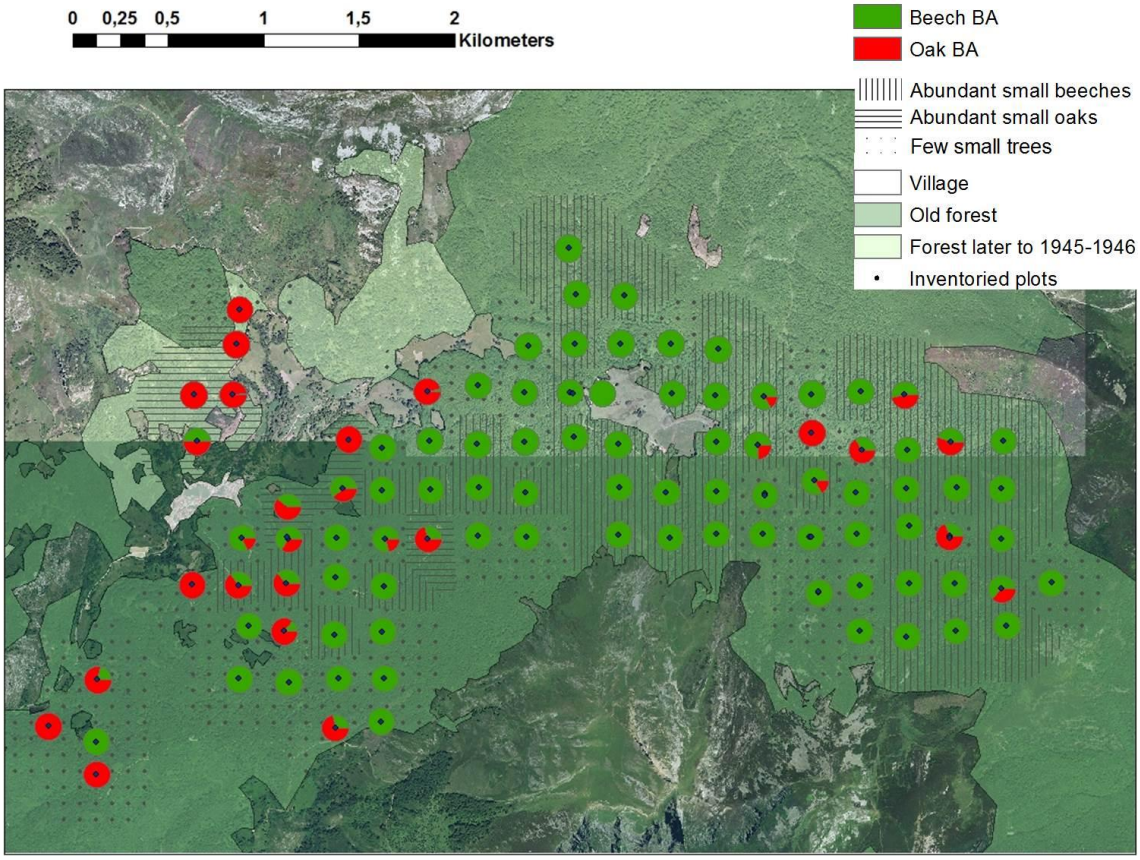

Figure 3.E.1. Map of the sampled area. Pies indicate the proportion of basal area by species. The areas marked as "abundant small beeches" have been obtained from the plots included in clusters P2 and M2. The areas marked as "abundant small oaks" have been obtained from the plots included in cluster M1. The areas marked as "few small trees" have been obtained from the plots included in clusters P1 and M3 (see **Table 3.1** and **Fig. 3.1**). The presence of a continuous forested area in this site was assessed by inspecting aerial photographs from 1945-1946 (PNOA, Instituto Geográfico Nacional, Spain).

Appendix F

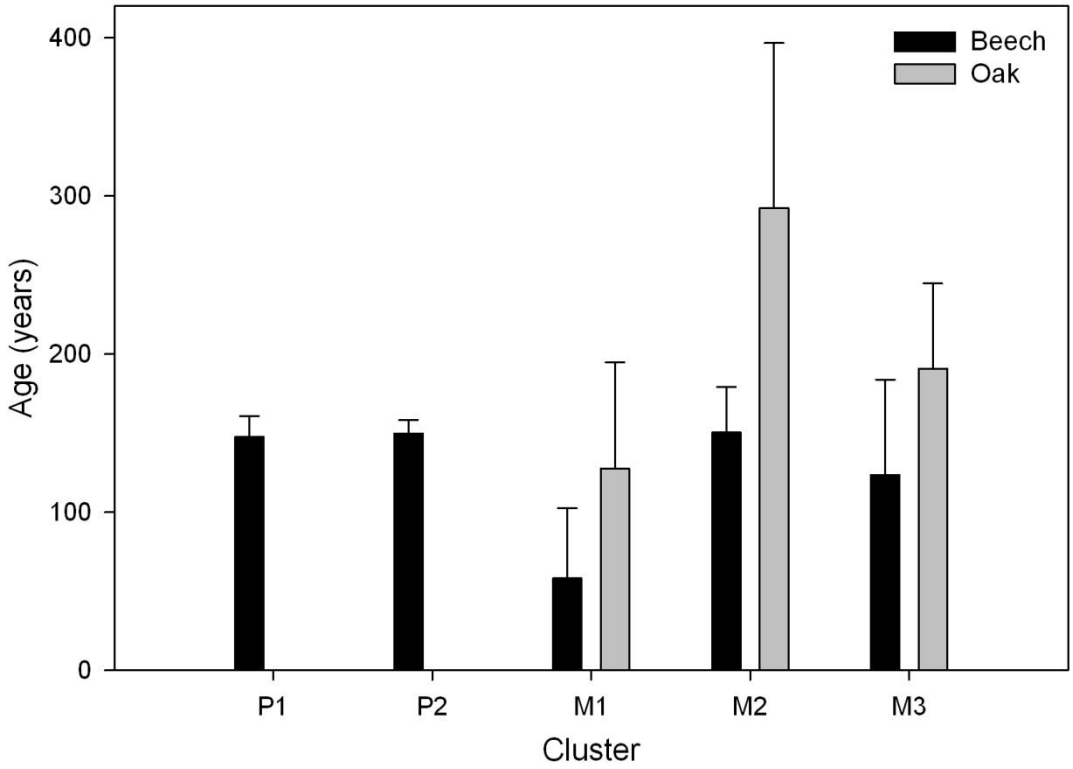

Figure 3.F.1. Comparison of mean ages between clusters (clusters's names are as in **Table 3.1**). Error bars indicate the 95% confidence intervals.

CAPÍTULO 4. COMPETITION OVERRIDES CLIMATE AS TRIGGER OF GROWTH DECLINE IN A MIXED FAGACEAE MEDITERRANEAN REAR-EDGE FOREST

Este capítulo reproduce el texto del siguiente artículo ya publicado:

Rubio-Cuadrado, Á., Camarero, J.J., Gordaliza, G.G., Cerioni, M., Montes, F., Gil, L., 2020. Competition overrides climate as trigger of growth decline in a mixed Fagaceae Mediterranean rear-edge forest. Ann. For. Sci. 77, 94. https://doi.org/10.1007/s13595-020-01004-5

Abstract

Context: In recent decades, two major factors have influenced tree growth in many forests: climate warming, which is associated with aridification and negative growth trends in many Mediterranean forests, and abandonment of forest management, resulting from forest policy in conjunction with rural depopulation in Europe, often leading to an increase in competition and a decrease in growth.

Aims: Here we study growth trends in a mixed forest of *Fagus sylvatica*, *Quercus petraea* and *Quercus pyrenaica,* where the abandonment of traditional uses in the 1960s has been followed by an increase in tree density. In this forest, both *F. sylvatica* and *Q. petraea* reach their south-westernmost limits of distribution.

Methods: Using dendrochronological methods and growth modeling, we assess the importance of climate warming on the shifts in competitive growth advantage of these three coexisting tree species and the relative importance of climate and competition on growth trends.

Results and conclusions: Q. petraea and especially *F. sylvatica*, showed favorable evolution of their competitive capacity, despite the increase in temperatures that has occurred in the area in recent decades. *F. sylvatica* presented the lowest sensitivity to climate. Under the current climate and forest structure conditions, competition is the most limiting factor on tree growth for the two oak species.

4.1. Introduction

The last 30-year period has been the warmest on the Earth's surface since 1850 (IPCC 2014). The Mediterranean region has been severely affected by this warming, which has brought about aridification of extensive drought-prone areas (Jacob et al. 2014). Climate change will particularly affect temperate and Mediterranean forests located at the equatorial limit (rear edge) of the tree species distribution (Hampe and Petit 2005). This is the case of certain hardwood tree species (oaks, beech) which form mixed forests in mountain areas of Spain under a typical sub-Mediterranean influence (Rubio-

Cuadrado et al. 2018c), characterized by warmer and drier conditions in summer (Giorgi and Lionello 2008).

Climate change is already affecting forest growth and productivity (Reyer et al. 2014). Negative growth trends associated with climate warming have previously been described in several Mediterranean conifer forests (Macias et al. 2006; Sarris et al. 2007, 2011; Gea-Izquierdo et al. 2014; Camarero et al. 2015), but temperate oak and beech forests with recurrent summer droughts typical of the Mediterranean climate are also negatively impacted (Piovesan et al. 2008; Colangelo et al. 2017; Dorado-Liñán et al. 2017a). These negative growth trends are forecasted to increase over the course of the 21st century (Sánchez-Salguero et al. 2017). Indeed, the Iberian Peninsula has been described as the most sensitive region, and that which is most likely to suffer the largest decreases in forest productivity throughout the continent (Morales et al. 2007; Reyer et al. 2014).

It is unclear how mixed forests subjected to summer drought will be able to cope with the negative effects on growth of warmer and drier climate conditions. On the one hand, species mixing may improve the capacity of the forest to recover after disturbances (i.e. larger resilience: Pretzsch et al. 2013). This is due to resource-use efficiency, which should enhance tree growth and stand productivity as a result of niche complementarity and facilitation between coexisting tree species (Richards et al. 2010). On the other hand, climate warming may favor species which are more adapted to drier and warmer conditions over typical temperate species (Rubio-Cuadrado et al. 2018b).

In addition to climate change, land-use changes have also affected growth trends in European forests (Linares et al. 2009; Camarero et al. 2011). In recent decades, forest policy in Europe has moved towards minimal intervention or non-management for several different reasons: aiming to increase adaptability and resilience (Brang et al. 2014), for conservation purposes or due to the low economic value of forest resources (Moreno-Fernández et al. 2016). However, most European forests have a long history of anthropogenic transformations (Valbuena-Carabaña et al. 2010; Schoolman et al. 2018), and are composed of relatively young stands. In

addition, during recent decades, forests have expanded into new areas, especially in Europe, mainly due to land use changes and afforestations, as well as to climate warming; all these new woodlands also being at early successional stages (Álvarez-Martínez et al. 2014; Penniston and Lundberg 2014; Price et al. 2017). Climate and land use changes have increased the frequency of disturbances (e.g. forest fires), thus preventing forests from reaching latter serial stages (McLauchlan et al. 2020). In all these stands, natural dynamics has often led to an increase in tree density and tree-to-tree competition over recent decades, which can result in decreased tree growth (Voelker et al. 2008; Linares et al. 2010; Ruiz-Benito et al. 2013; Hosseini et al. 2018).

In this study, we analyze the growth trends in a mixed beech-oak forest ("El Hayedo de Montejo"; **Fig. 4.1**) dominated by *Fagus sylvatica* L., *Quercus petraea* (Matt.) Liebl. and *Quercus pyrenaica* Willd., with a long history of anthropogenic intervention (Pardo and Gil 2005). The studied forest harbors one of the southernmost (rear edge) and westernmost populations of *F. sylvatica* and *Q. petraea* in Europe, while in the case of *Q. pyrenaica* it is the core of its distribution range (Pardo et al. 2004). Since the 1960s, traditional uses (logging, grazing) have ceased in the study area, and this has promoted forest recruitment and densification, evolving from open woodland to a dense forest (Gil et al. 2009). Previous studies conducted at this site have shown a general decline in growth of the dominant trees, attributed to temperature increase over recent decades (Dorado-Liñán et al. 2017a). The effect of competition on dominant trees is often neglected in dendroecological analyses, but substantial increases in density may reduce the resources available not only to dominated or suppressed trees, but also to dominant trees, leading to growth decline. However, the complexity involved in disentangling the combined effects of climate change and the recent evolution of the forest, in particular the increase in competition, has meant that this situation has not yet been analyzed. The aim of this study is to evaluate the relative importance of climate and competition on the radial growth of dominant and co-dominant trees. Our specific objectives are: (1) to study the evolution of the competitive growth advantage of the three coexisting species; and (2) to analyze the relative importance of climate and competition on the radial growth of *F. sylvatica*, *Q. petraea* and *Q. pyrenaica* in this mixed forest. We hypothesize that:

(1) the increase in temperature and frequency of drought events have a positive effect on the growth of the Mediterranean species (*Q. pyrenaica*) but have a negative impact on that of the temperate species (*F. sylvatica* and *Q. petraea*); (2) increase in competition has been the main limiting factor on the growth of the three species over recent decades and (3) competition has a greater impact on *Q. pyrenaica* and *Q. petraea* than on the more competitive *F. sylvatica*. To fulfill the objectives and verify the hypothesis, we analyzed the relationships between climate, the tree-ring widths of the three species, and stand basal area. In order to evaluate the first hypothesis we used climate-growth correlations and pointer year analysis. To evaluate the first and third hypotheses the differences among the species, in terms of the long term growth response to the evolution of site conditions, were analyzed using the competitive advantage index based on radial-growth data (Rubio-Cuadrado et al. 2018b). Finally, to evaluate the second and third hypotheses, we analyzed the relative importance of competition and climate on basal area increment for the three species using mixed models.

4.2. Materials and methods

4.2.1. Study area

The study site, "El Hayedo de Montejo", is a mixed forest of 125 ha located in the Sistema Central mountain range, Central Spain (41° 07' N; 3° 30' W; **Fig. 4.1**), between 1,250-1,500 m a.s.l. The dominant species are *Fagus sylvatica* L. (hereafter beech), *Quercus petraea* (Matt.) Liebl. (hereafter oak) and the Mediterranean *Quercus pyrenaica* Willd., with a relative basal area of 27%, 23% and 50% and a mean diameter at breast height of 16.5, 19.9 and 24.1 cm, respectively. This forest is close to the southernmost European distribution limit of the two temperate species (beech and oak). The beech and *Q. petraea* trees in the studied forest come from natural seeding, as do most of the *Q. pyrenaica* individuals, in contrast to coppice stands, which characterize *Q. pyrenaica* in Central Spain (Valbuena-Carabaña et al. 2008). The forest has historically been exploited for firewood and cattle grazing, which originated an open woodland structure of dispersed large, mature trees with scarce tree

recruitment. However, for conservation purposes, cattle grazing has been forbidden in the forest since 1961 and the last logging operation was carried out in 1962 (López Santalla et al. 2003; Gil et al. 2009), favouring the increase in tree density and competition. In this regard, the inventories carried out in the forest in 1994, 2005 and 2015 (see section 4.2.3 *Tree sampling and competition data*), gave an average basal area for these years of 20.9, 26.5 and 28.8 m^2 ha^{-1}, respectively, and an average density of 616, 952 and 910 trees ha^{-1}, respectively.

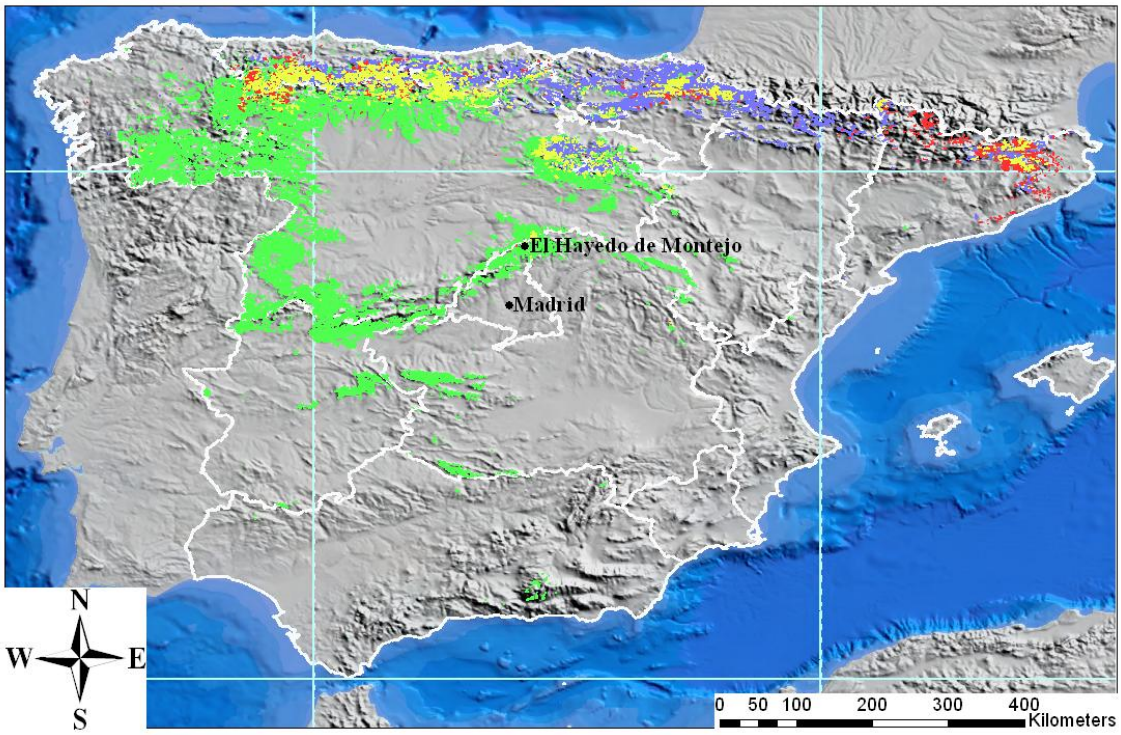

Figure 4.1. Map of the Iberian Peninsula with the distribution of *Fagus sylvatica* (blue color), *Quercus petraea* (red) and *Quercus pyrenaica* (green). Areas where at least two of the three species are mixed are represented in yellow. Sources: species distribution cartography has been elaborated by INIA-CIFOR from Third National Forest Inventory (https://www.miteco.gob.es/es/biodiversidad/servicios/banco-datos-naturaleza/informacion-disponible/ifn3.aspx) and Digital Terrain Model has been elaborated by © Instituto Geográfico Nacional.

The site has a Mediterranean continental climate with 900 mm mean annual rainfall and a prolonged dry period during July and August (Gil et al. 2009). The mean annual temperature is around 9.5 ºC (climate data from the meteorological station of

the “Natural Systems and Forest History” research group of the Universidad Politécnica de Madrid, located within the studied forest). The soil is classified as humic cambisol (Pardo et al. 1997) and the A horizon reaches an average depth of 50 cm which allows water to be stored during dry periods.

4.2.2. Climate data

Local climate data from the “Pantano El Vado” weather station (41° 0’ 13’’ N and 3° 18’ 7’’ W, 910 m a.s.l., AEMET, Spanish Meteorological Agency) located at ca. 21 km from the forest was used in this study. Missing monthly temperature and precipitation data as well as daily temperature data were estimated using linear regressions, which relate climatic variables from this station with the temperatures from “Puerto de Navacerrada” weather station (AEMET, 40° 47’ 35’’ N, 4° 0’ 38’’ W, 1894 m a.s.l.) and with precipitation data from “Arbancón” weather station (AEMET, 40° 58’ 0’’ N, 3° 6’ 57’’ W, 902 m a.s.l.) as follows:

$$MT_{\text{Pantano El Vado}} = 0.9786 * MT_{\text{Puerto de Navacerrada}} + 5.8616 \quad (1)$$

$$DT_{\text{Pantano El Vado}} = 0.847 * DT_{\text{Puerto de Navacerrada}} + 6.7033 \quad (2)$$

$$MP_{\text{Pantano El Vado}} = 1.2395 * MP_{\text{Arbancon}} + 3.9396 \quad (3)$$

where MT, MP and DT and are the monthly data for temperature and precipitation and the daily data for temperatures, respectively. $R^2 = 0.96$ for eq. 1, $R^2 = 0.83$ for eq. 2 and $R^2 = 0.76$ for eq. 3. For the missing daily precipitation data from the "Pantano El Vado" local station we used the daily data from "Arbancón" weather station (directly, without transforming) due to the low R^2 (0.13) regression line that relates both data series given the high spatial variability intrinsic to this variable.

In addition, to assess drought intensity we used the Standardised Precipitation-Evapotranspiration Index (SPEI) (Vicente-Serrano et al. 2010b, a) calculated from the same local data using the Thornthwaite equation to estimate potential evapotranspiration within the *SPEI* package in R (Beguería and Vicente-Serrano 2017).

The SPEI drought index considers the effect of temperature on evapotranspiration rates and the cumulative water deficit. High and low SPEI values correspond to wet and dry conditions, respectively. The period from the arrival of water input (precipitation) to availability of a given usable resource (water absorption by the roots) differs considerably. Thus, the time scale over which water deficits accumulate becomes extremely important to calculate the SPEI. For this reason we used a range of time scales (from 1 to 20 months) during which the water deficit and surplus are accumulated (Vicente-Serrano et al. 2010b).

4.2.3. Tree sampling and competition data

Three forest inventories were carried out in 1994, 2005 and 2015 in the studied forest. In each inventory, 125 circular plots systematically distributed on a square grid of 100 m × 100 m were established covering the entire forest area. Permanent plots have been established since 2005, so the plots in the second and third inventories were at the same locations, whereas in 1994 the locations were different, although the area covered and the sampling intensity were the same. Based on the 2015 inventory data, all plots with mixed forest (presence of at least two of the three studied species) were selected for the extraction of two cores at 1.3 m (always perpendicular to the maximum slope) from a dominant or codominant tree of each species located nearest to the plot center using a Pressler increment borer. The diameter at breast height (DBH) of each tree bored was measured at 1.3 m with a caliper. Sampling took place during autumn of 2018. At least 20 trees per species, distributed across 32 plots, were sampled.

Total stand basal area (BA) and the fraction of it belonging to each of the species were calculated in 12.6 m radius plots for the 1994, 2005 and 2015 inventories. The area of the plot with this radius is slightly larger than the crown projection of these species, in accordance with the DBH-crown diameter relationship of the Second Spanish National Forest Inventory (DGCONA 1998), so the BA estimated can be considered an indicator of stand level competition for resources. Spatio-temporal Universal Kriging (UK) was used to interpolate the total BA and spatio-temporal

Ordinary Kriging (OK) to interpolate the proportion of each species for the 1994-2015 period from the BA measured in the inventory plots. As vegetation indices can indicate changes in stand density (Gómez et al. 2012), Normalized Difference Vegetation Index (NDVI) averaged from the available Landsat images for July-August of each year was used as an auxiliary variable in the UK interpolation of BA. These models interpolate the BA value and the proportion of each species at the plot locations for each year of the 1994-2015 period using the spatial and temporal autocorrelation of the variables to determine the optimal kriging weights. The low annual growth rates of the three analyzed species in the study area along with the species regeneration and development processes result in a high spatio-temporal autocorrelation of BA at the distance and time lags between measurements (100 m distant sampling plots and 10 years between inventories), providing consistent interpolated values for the 1994-2015 period. The spatio-temporal autocorrelation was modeled through the generalized product-sum variogram model (De Iaco et al. 2002). The OK variogram parameters were estimated using Weighted Least Squares (Cressie 1985), whereas the UK variogram parameters and mean function coefficients were estimated through the Iteratively Reweighted Generalized Least Squares method proposed by Neuman and Jacobson (1984). Cross validation was carried out to verify the unbiasedness of the estimated values and the ratio between the estimated kriging variance and the mean of the cross validation squared residuals. Competition data are available in Rubio-Cuadrado et al. (2020) (https://doi.org/10.21950/VEQWPI).

4.2.4. Radial growth data

Cores of the sampled trees were mounted on wooden supports and carefully sanded until tree rings were clearly visible. After visual cross-dating, tree-ring widths (TRW) were measured to the nearest 0.01 mm using the semi-automatic LINTAB measuring device with the TSAP-Win software (RINNTECH, Heidelberg, Germany). Cross-dating was then further verified using the COFECHA program (Holmes 1997). A beech sample, with a very different age (129 years) and growth trend and very low correlation with

the mean species series (close to 0), was discarded from further analysis. TRW data are available in Rubio-Cuadrado et al. (2020) (https://doi.org/10.21950/VEQWPI).

We calculated the mean growth series for each individual, and these series were subsequently transformed into basal area increments (BAI) as this variable is better than tree-ring width for capturing growth trends and accounting for the increase in size and age of stems (Biondi and Qeadan 2008). The BAI was calculated as follows:

$$BAI = \pi(r_t^2 - r_{t-1}^2) \quad (4)$$

where r_t and r_{t-1} are the stem radii at the end and the beginning of a given annual ring increment corresponding to rings formed in *t* and *t*-1 years, respectively.

When the cores did not contain the pith, the length of the missing radius was estimated to calculate the BAI as the distance to the geometric center of the tree, assuming concentric growth. Estimation was carried out by subtracting the corresponding cored length to the measured radius in the field, previously subtracting an estimated width of the bark. Bark thickness was estimated based on tree diameter using equations obtained from the data of the Second Spanish National Forest Inventory (DGCONA 1998). The functions used to estimate the bark thickness of *F. sylvatica* (C_{Fs}), *Q. petraea* (C_{Qpe}) and *Q. pyrenaica* (C_{Qpy}) are the following:

$$C_{Fs} = -0.00001\ DBH^2 + 0.0284\ DBH + 0.3545 \quad (5)$$

$$C_{Qpe} = 1.4407\ DBH^{0.4071} \quad (6)$$

$$C_{Qpy} = 7.4422\ \ln(DBH) - 23.845 \quad (7)$$

The final species chronologies were built by averaging all individual BAI measurements of the same species. The statistical quality of each chronology was checked via Expressed Population Signal (EPS) (**Table 4.1**). The sample depth is considered adequate when EPS>0.85 (Speer 2012).

Pointer years (years with anomalistically low BAI) are ecological indicators recording the reaction of the trees to environmental stress factors (Schweingruber et

al. 1990). Based on previous studies (Rubio-Cuadrado et al. 2018c, a; Nechita et al. 2019) negative pointer years were determined as those years in which at least 60% of the BAI series of one species showed a decrease in BAI of at least 40% relative to the average BAI in the 4 preceding years. The growth response to these unfavorable years and the ability to recover pre-disturbance growth levels after the disturbance were estimated for the tree-ring series through the resistance (*Rt*) and resilience (*Rs*) indices (Lloret et al. 2011):

$$Rt = BAI_i / BAI_{i-4} \quad (8)$$

$$Rs = BAI_{i+4} / BAI_{i-4} \quad (9)$$

where BAI_i is the BAI value of the *i* year. These indices were calculated with 4-year pre- (*i*-4), and post-disturbance (*i*+4) periods using the *pointRes* package in R (van der Maaten-Theunissen et al. 2015).

Table 4.1. Description of dendrochronological variables of cored trees. Statistics were calculated for the maximum series length for each species. Standard errors are shown in parentheses.

	F. sylvatica	***Q. petraea***	***Q. pyrenaica***
No. cored trees	20	22	20
Mean DBH (cm)	28.6 (1.0)	32.8 (1.3)	33.6 (2.5)
Mean / maximum length of series (years)	45 (1) / 56	45 (1) / 59	64 (7) / 143
Mean tree-ring width (mm)	2.51 (0.04)	2.74 (0.04)	1.77 (0.03)
Mean basal area increment (cm^2)	10.6 (0.3)	13.4 (0.3)	10.5 (0.2)
Mean basal area increment since 1971 (cm^2)	11.7 (0.3)	15.4 (0.3)	10.6 (0.2)
Mean correlation between trees	0.34	0.29	0.17
Expressed Population Signal since 1971	0.95	0.94	0.88

4.2.5. Climate-growth relationships

Since the BAI may contain long-term trends due to non-climate factors, i.e. competition, to determine the main climatic drivers of tree growth we used ring-width indices (RWI), removing the biological trends of the raw tree-ring widths (TRW) for each species using the ARSTAN program (Holmes 1997). We used a double detrending

procedure to remove long-term growth trends (Holmes et al. 1986). First, we fitted a negative exponential curve to the TRW to remove the age effect in the first years of the growth series because of the low competition associated with the open woodland conditions during the establishment period of the analyzed trees, and second, we fitted a 32-year cubic smoothing spline to remove the low-frequency stand dynamics signals. In order to retain climatically-related autocorrelation in growth, part of this signal was reintroduced into the residual time series by applying a first-order autoregressive model. Pearson correlation coefficients were then calculated for that period with more than ten samples per species, i.e. for the period 1971-2015, between the RWI (mean series of the detrended TRW) of each tree species and temperature and precipitation grouped on daily or alternatively, on monthly basis. We tested the Pearson correlations between RWI and all possible climate window widths (periods of year) at daily resolution using the *dendroTools* package in R (Jevšenak and Levanič 2018). We summarize the climate variables in the selected time window, using mean and sum for temperature and precipitation, respectively. We fixed a 30-day threshold as the minimum widths of the climate window in order to reduce the total number of calculated correlations and therefore the probability of obtaining spurious correlations. Correlation coefficients between RWI and monthly temperature and precipitation were calculated from June of the previous year to November of the growth year considering that: (i) climate during the previous year affects growth during the following year (Fritts 1976), and (ii) growth in the two *Quercus* species can occur until November (Pérez-de-Lis et al. 2017). Pearson correlations were also calculated between the detrended growth series and the SPEI using time scales from 1 to 20 months (see section 4.2.2 *Climate data*).

4.2.6. Retrospective analyses of species competitive dynamics

To study the specific signals of growth patterns of the three studied species and to analyze their differences, we used the competitive advantage index (CA) based on radial-growth data (Rubio-Cuadrado et al. 2018b). This was based on the assumption that for trees of the same species growing in similar conditions of soil, competition,

etc., higher growth values imply higher competitive ability (Weber et al. 2008). The CA index was used to compare the percentage of trees of two species showing increasing growth in five-year intervals. In this way, we are able to study changes in the growth trends (due to climate or other factors) that benefit some species over others. Indeed, a species that maintains a constant downward trend in its relative growth will end up being dominated, benefiting the other competing species. However, this index does not consider other aspects of species competitiveness, such as re-sprouting capacity, carbon storage, seed dispersion capacity and shade tolerance.

In order to obtain the CA index, firstly the BAI series of all trees were smoothed, calculating them for 5-year moving intervals since we were interested in the long-term growth trends. Secondly, the number of ascending increments of BAI between consecutive years was summarized for each species. This was then transformed to percentages for species and year (i.e. percentage of trees of *F. sylvatica*, *Q. petraea* and *Q. pyrenaica* with ascending increments in the 5-year BAI series between two consecutive years) to give a relative series of competitive ability over time. To calculate the competitive advantage series of *F. sylvatica* over *Q. petraea* ($CA_{Fsyl\text{-}Qpet}$), the percentage series of competitive ability for *Q. petraea* was subtracted from the percentage series of competitive ability for *F. sylvatica*. In the resulting competitive advantage series, positive values indicate competitive advantage for *F. sylvatica*, whereas negative values indicate competitive advantage for *Q. petraea* (Rubio-Cuadrado et al. 2018b). Competitive advantage series for *F. sylvatica* over *Q. pyrenaica* ($CA_{Fsyl\text{-}Qpyr}$) and for *Q. petraea* over *Q. pyrenaica* ($CA_{Qpet\text{-}Qpyr}$) were calculated in the same way.

To calculate the relationships between $CA_{Fsyl\text{-}Qpet}$, $CA_{Fsyl\text{-}Qpyr}$, $CA_{Qpet\text{-}Qpyr}$ and climate, annual series of monthly temperature and precipitation were smoothed using a 5-year moving average. Pearson correlation coefficients between the CA and the smoothed series of climate variables from June of the previous year to November of the growth year were calculated. To calculate the *p*-values of these correlations we corrected the degrees of freedom, which decrease due to the repeated use of the same data in the moving-average series (Munshi 2016). We also grouped monthly climatic data into seasons to better reflect the relationships between competitive

advantage and seasonal climate conditions. The correlations between the CA series and the climatic variables series were analyzed between 1971 and 2015.

4.2.7. Factors influencing the radial growth of tree species

We used linear mixed-effects models to evaluate BAI trends of *F. sylvatica*, *Q. petraea* and *Q. pyrenaica* with the following variables included in the saturated models as predictors or fixed factors: DBH of the cored tree at the year of each annual radial growth (annual DBH), as most of the growth variance is explained by tree size (Monserud and Sterba 1996; Cescatti and Piutti 1998; Diaconu et al. 2015); total plot basal area (BA) and the fraction of it belonging to each of the species at the year of each annual radial growth (kriging estimates of annual values at the sampling points), to study the influence of the competition; and the monthly climate variables showing significant correlations with growth for each species (temperatures of March of the current growth year and precipitations from June to October of the previous year and of April of the current year in the *F. sylvatica* model; temperatures from June to July of the current year and precipitations from July to September of the previous year and from April to July of the current year in the *Q. petraea* model, and temperatures of November of the previous year and June of the current year and precipitations from July to September of the previous year and from April to July of the current year in the *Q. pyrenaica* model). Instead of the previous monthly climate variables, we have also tried to introduce, as fixed effects, the temperature and precipitation periods that best correlates with growth for each species using daily resolution (**Table 4.2**); however the resulting models explained less (in the case of *F. sylvatica*) or similar (in *Q. petraea* and *Q. pyrenaica*) variability so, to avoid mixing climate data with different temporal resolutions, only the monthly climate data were used in the final models. Only tree identity was considered as a random component of the models (1|Tree). We considered all the period with available competition and growth data (1994–2015).

To predict BAI we adjusted the following linear mixed-effects model with random intercept and fixed slope:

$$y_{ij} = \alpha + a_j + \beta z_{ij} + \varepsilon_{ij} \quad (10)$$

where y_{ij} represents log (BAI + 1) for year i and tree j, α is the general intercept, a_j is the random intercept (tree identity), β is the vector of general slopes, z_{ij} is the vector of fixed effects, and ε_{ij} is the error with a first-order temporal autocorrelation [AR(1)] structure. We used log-transformed (BAI + 1) data because BAI had a Gamma distribution. The distribution was tested using the Kolmogorov-Smirnov test.

To identify the best-supported model we constructed all possible combinations of alternative models from the full model considering fixed and random effects and the interactions between the fixed effects. As the restricted maximum likelihood method (REML) estimates an unbiased variance, but does not allow models to be compared by minimizing the Akaike Information Criterion (AIC), we first fitted all possible models using the Maximum Likelihood method (ML), then selected the best model by minimizing AIC and finally fitted it again using the restricted maximum likelihood method (REML) (Zuur et al. 2009). The use of the AIC was considered equivalent to using cross-validations to validate mixed effects models (Fang 2011). The existence of multicollinearity among explanatory variables was evaluated by calculating the variance inflation factor (VIF). VIF values greater than 10 mean that there is high collinearity among variables (Dormann et al. 2013). The percentages of variance explained by fixed (R^2_m, marginal R^2) and fixed plus random (R^2_c, conditional R^2) factors were obtained following Nakagawa and Schielzeth (2013).

To study the effect of each variable on tree growth, we used the linear mixed-effects model fitted for each species to predict the evolution of the BAI according to the variation of each variable separately and fixing (as constants) the rest.

4.3. Results

4.3.1. Climate trends

The climate data did not show a significant trend when we considered the whole period. However, since 1976, there has been a significant (P < 0.01) temperature increase of +0.022 ºC yr^{-1} (**Fig. 4.2**).

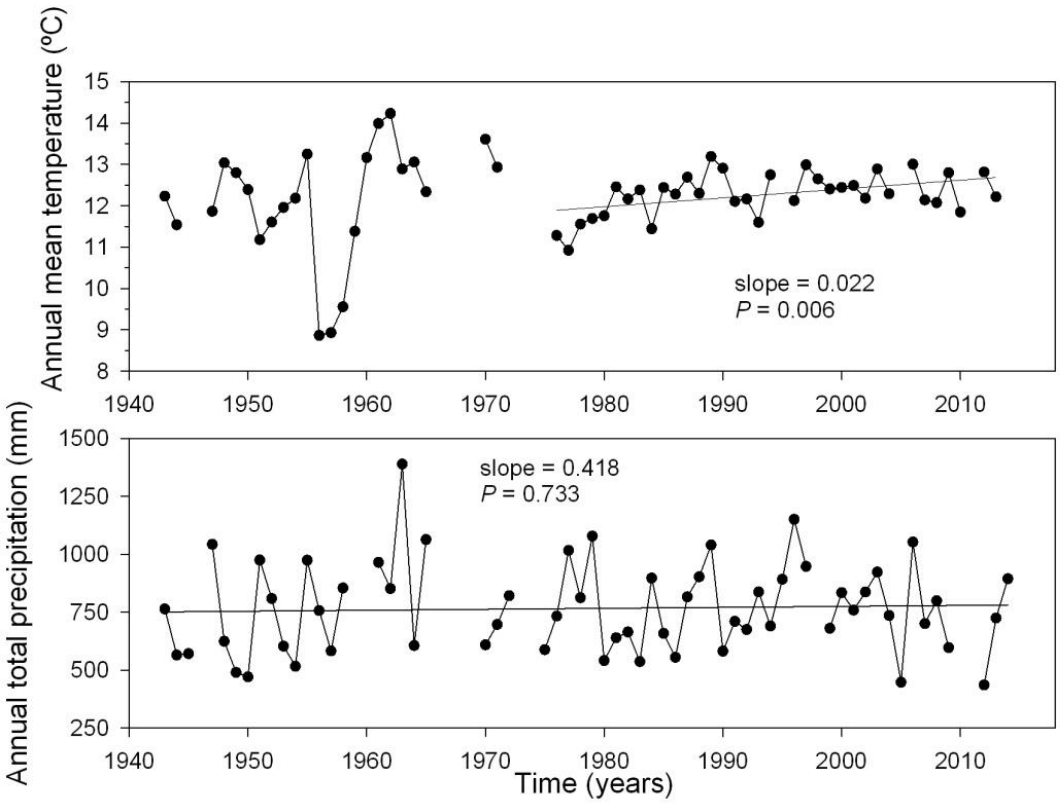

Figure 4.2. Climatic trends (annual mean temperature and total precipitation) in the study area (data of the "Pantano El Vado" AEMET station). The slopes of the simple regressions fitted to temperature (from 1976 to 2013) and precipitation (from 1943 to 2014), respectively, are shown.

4.3.2. Growth trends

The three studied species had two clearly differentiated periods according to their growth patterns: an ascending growth trend between 1971 and 1990, and a decreasing (in *Q. petraea* and more sharply in *Q. prenaica*) or stable (*F. sylvatica*) growth trend from 1990 onwards (**Fig. 4.3**). The growth changes in *F. sylvatica* and *Q. petraea* were very similar over time, their growth curves being almost parallel. However, since 1995 *Q. petraea* growth has shown a slightly decreasing trend while *F. sylvatica* has shown an increasing or stable growth trend, matching the growth of both species between 2007-2009, although this suddenly decrease in 2010 and notably since 2015. The spline adjusted to the beech BAI decreases at the end of the period studied due to a sharp drop in growth caused by a spring frost in 2017, which severely damaged the leaves as they were unfolding.

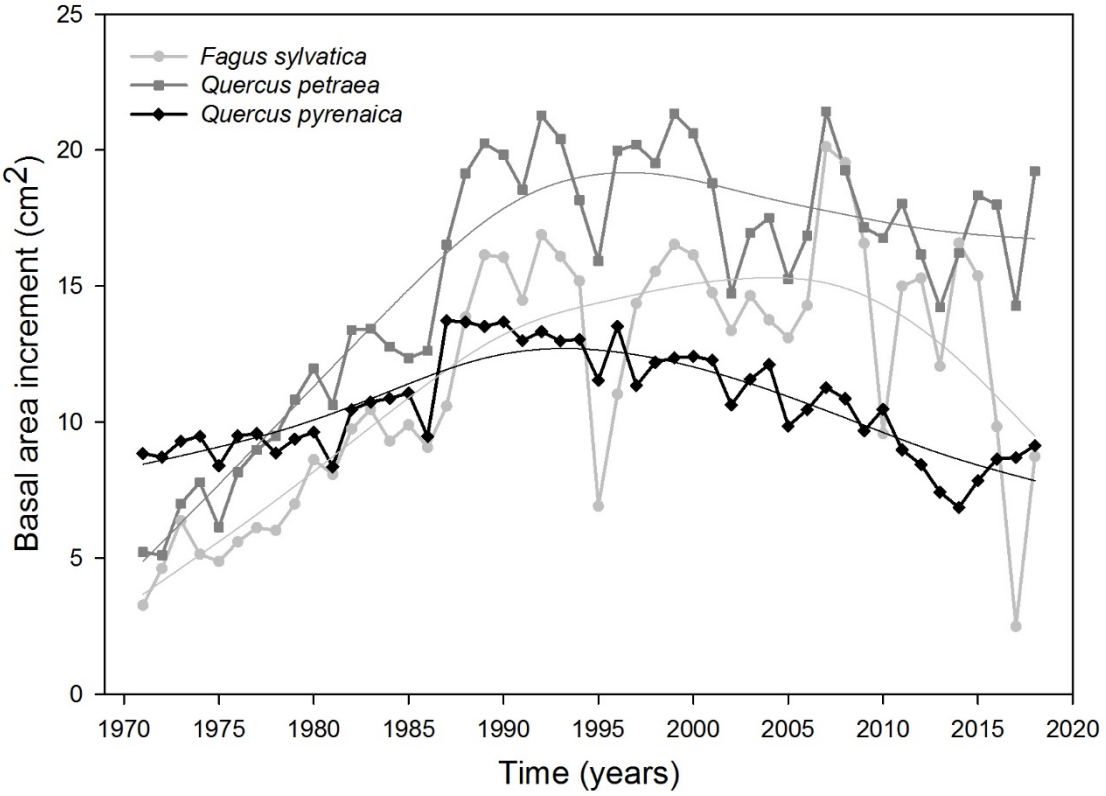

Figure 4.3. Growth (BAI, basal area increment) of the three species studied since 1971. We fitted a 30-year long cubic smoothing spline for each species to highlight BAI decadal to multi-decadal variations. The rigidity of the splines was chosen

visually. Note the sharp BAI drop in 2017 observed in beech due to a spring frost.

4.3.3. Climate-growth relationships

The growth of *F. sylvatica* was directly related to the mean temperature of March of the current growth year (r = 0.29, P < 0.05) and to the total precipitation from June to October of the previous year (r = 0.32, P < 0.05) (**Fig. 4.4**). Climate-growth correlations were similar in both *Quercus* species. Growth of the oak (*Q. petraea*) was inversely related to the mean temperature from June to July of the current growth year (r = -0.35, P < 0.05), and directly related to the total precipitation from July to September of the previous year (r = 0.43, P < 0.01), and from April to July of the current year (r = 0.50, P < 0.01). Similarly, the growth of *Q. pyrenaica* was directly related to the total precipitation from July to September of the previous year (r = 0.33, P < 0.05), and from April to July of the current year (r = 0.44, P < 0.01). Using a daily climate resolution, the periods that showed the greatest correlation with the growth of *F. sylvatica* were September 29 - October 28 for temperature and April 04 - May 05 for precipitation (**Table 4.2**). In *Q. petraea* the periods were June 11 - July 17 for temperature and April 04 - September 16 for precipitation and in *Q. pyrenaica* the periods were March 17 - April 15 for temperature and May 13 - September 11 for precipitation.

Table 4.2. Optimal climate windows (window width with the maximum correlation), window lengths in days, Pearson correlation coefficients and associated probability levels (P) calculated between the ring-width indices (RWI) and climate variables. Temperature and precipitation variables are the averaged and total values of the grouped days, respectively.

Species	Variable	Climate window	Days	Correlation	*P*-value
F. sylvatica	Temperature	Sep. 29 - Oct. 28	30	-0.338	0.019
F. sylvatica	Precipitation	Apr. 04 - May 05	32	0.327	0.023
Q. petraea	Temperature	Jun. 11 - Jul. 17	37	-0.365	0.011
Q. petraea	Precipitation	Apr. 04 - Sep. 16	166	0.453	0.001
Q. pyrenaica	Temperature	Mar. 17 - Apr. 15	30	-0.355	0.013
Q. pyrenaica	Precipitation	May 13 - Sep. 11	122	0.408	0.004

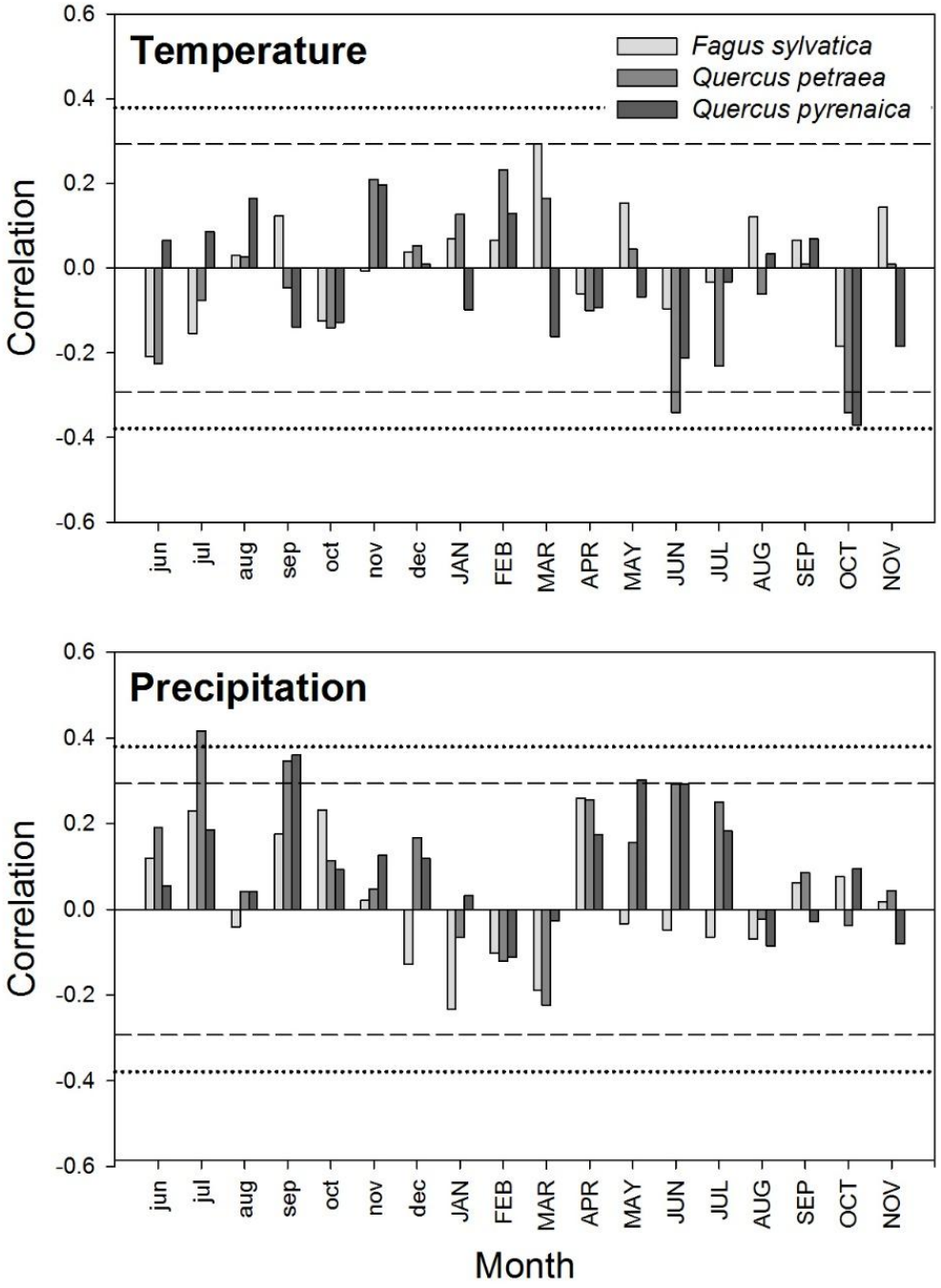

Figure 4.4. Climate-growth relationships based on Pearson coefficients and calculated by relating ring-width indices (RWI) to monthly mean temperature and total precipitation. Months with lowercase letters correspond to the previous year. Horizontal dashed and dotted lines indicate significant correlations at $P < 0.05$ and $P < 0.01$, respectively.

Only the *Quercus* species showed significant correlations with the SPEI drought index (**Fig. 4.5**). The highest correlations with SPEI corresponded to *Q. pyrenaica*. The growth of *Q. petraea* was negatively affected by the cumulative drought severity from March to October of the growth year, whereas the growth of *Q. pyrenaica* was affected by the cumulative drought severity from April to September.

F. sylvatica was the only species which presented pointer years, which were 1995 and 2017. Resistance was 0.45 and 0.18 for the years 1995 and 2017, respectively, and resilience was 0.81 for the year 1995. The resilience for the year 2017 could not be calculated because we only had growth data up to the year 2018. There were spring frosts in both 1995 and in 2017.

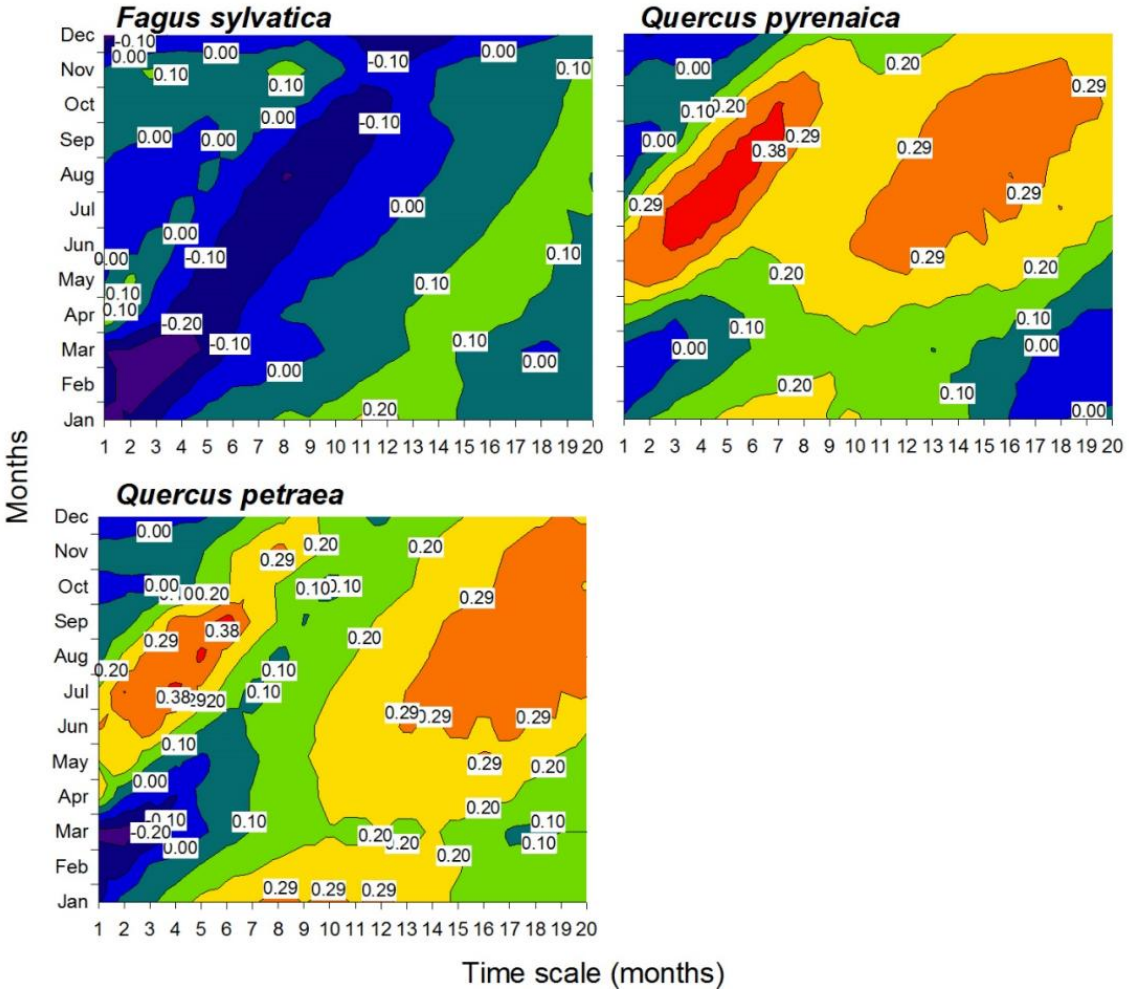

Figure 4.5. Pearson correlations calculated between the ring-width indices (RWI) and the SPEI drought index from January to December (*y* axes) and for time scales between 1 and 20 months (*x* axes). Correlation values higher than 0.29 and 0.38 are significant at $P < 0.05$ and 0.01, respectively.

4.3.4. Retrospective analyses of species competitive dynamics

During the study period, there were alternating periods of competitive advantage for one or other of the studied species (**Fig. 4.6**). In general, we observed no clear trends of the competitive advantage series, except in recent years when the competitive advantage of *F. sylvatica* over both *Quercus* species ($CA_{Fsyl\text{-}Qpet}$ and $CA_{Fsyl\text{-}Qpyr}$) showed a negative trend due to the effects of the spring frost of 2017. However, *F. sylvatica* showed increasing growth for a higher percentage of trees than *Q. petraea* and *Q. pyrenaica* (i.e. $CA_{Fsyl\text{-}Qpet}$ or $CA_{Fsyl\text{-}Qpyr} > 0$) in 67% and 65% of the years, respectively, with average values for the competitive advantage series of 5.5% ($CA_{Fsyl\text{-}Qpet}$) and 10.8% ($CA_{Fsyl\text{-}Qpyr}$). Although the percentage of trees of *Q. petraea* with increasing growth was only larger than that of *Q. pyrenaica* in half of the years, the average value of the $CA_{Qpet\text{-}Qpyr}$ was 5.3%.

Precipitation from May to June was inversely related with the competitive advantage of *F. sylvatica* over *Q. petraea* (**Table 4.3**). The temperature from June to July was also inversely related with the competitive advantage of *Q. petraea* over *Q. pyrenaica* while precipitation of February and June were directly related with this advantage. There were no significant correlations of $CA_{Fsyl\text{-}Qpyr}$ with the climate variables.

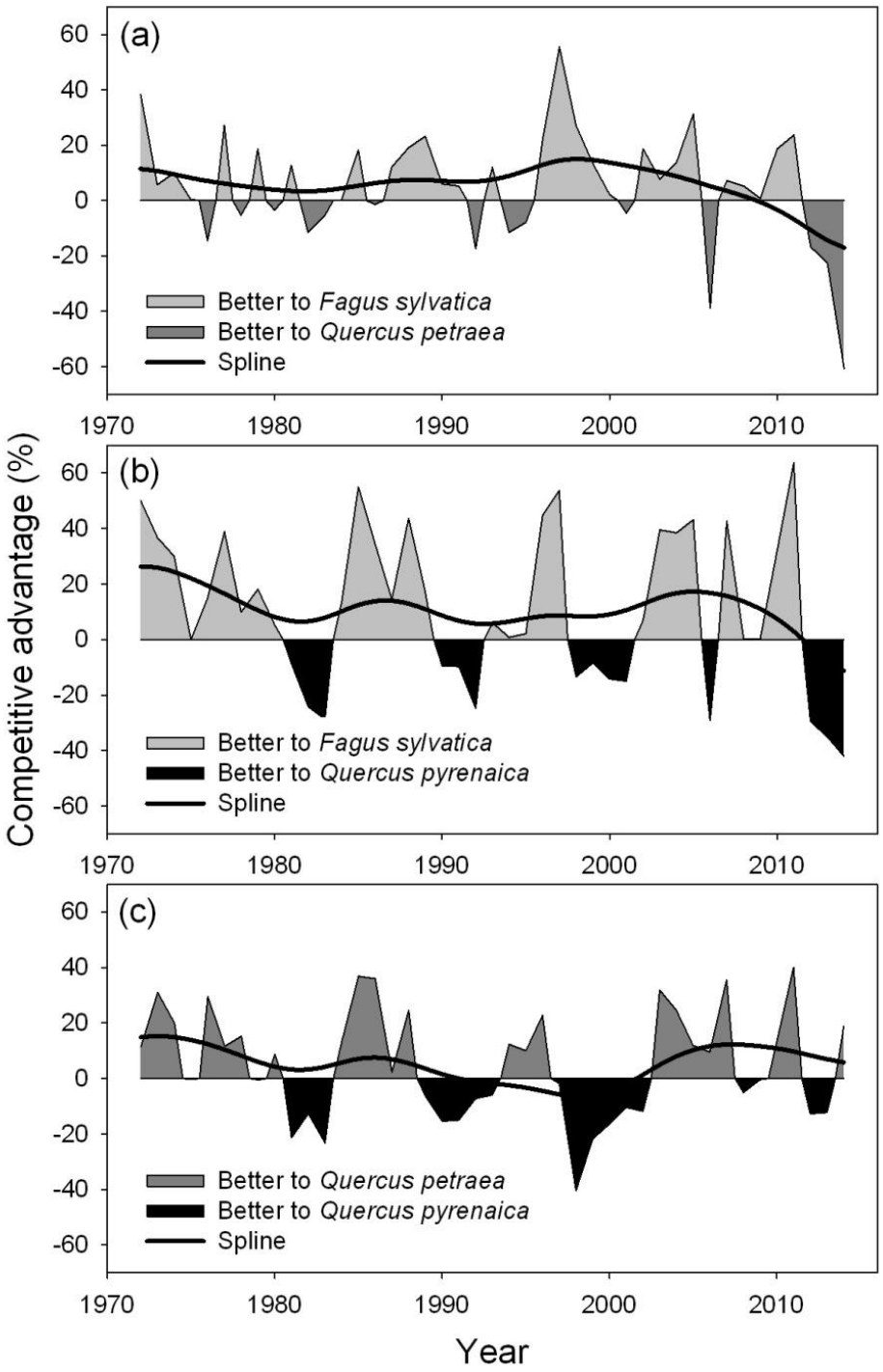

Figure 4.6. Reconstructed competitive advantage (CA) series of *Fagus sylvatica* over *Quercus petraea* (a, $CA_{Fsyl\text{-}Qpet}$), *Fagus sylvatica* over *Quercus pyrenaica* (b, $CA_{Fsyl\text{-}Qpyr}$) and *Quercus petraea* over *Quercus pyrenaica* (c, $CA_{Qpet\text{-}Qpyr}$) from 1971 to 2018. We fitted a 30-year long cubic smoothing spline for each CA to show the decadal to multi-decadal variations. The rigidity of the splines was visually chosen.

Table 4.3. Pearson correlation coefficients and associated probability levels (*P*) calculated between the different competitive advantage (CA) series and climate variables. Temperature and precipitation variables are the averaged and total values of the grouped months, respectively.

CA	Climate variable	Correlation	*P* value
$CA_{Fsyl\text{-}Qpet}$	$Precipitation_{from\ May\ to\ June}$	-0.41	< 0.05
$CA_{Qpet\text{-}Qpyr}$	$Temperature_{from\ June\ to\ July}$	-0.33	< 0.10
	$Precipitation_{February}$	0.47	< 0.05
	$Precipitation_{June}$	0.40	< 0.05

4.3.5. Factors influencing species growth trends

In the three growth models (**Table 4.4** and **Fig. 4.7**), the VIF of all predictors were lower than 3, so collinearity was assumed to be low. According to these models 38.8% (for *F. sylvatica*), 14.2% (for *Q. petraea*) and 12.1% (for *Q. pyrenaica*) of the BAI variability remained unexplained. Similarly, 30.7%, 38.1% and 36.5% of the variability in each of these species, respectively, was explained by fixed factors (R^2_m), and 30.5%, 47.7% and 51.4% of the variability (R^2_c) was explained by differences between trees (soil, orientation, slope, altitude, genetics, vigor, etc.).

In the beech growth model there was an interaction between April precipitation and mean March temperature. According to this interaction, when one of the two variables had low values (low temperature or low precipitation), as the value of the other variable increased, growth also increased (**Fig. 4.7**). However, when one of the variables showed high values, the other variable had no significant effects (note the width of the confidence interval for this case).

The three BAI models presented a good fit, although in both *Quercus* models the fitted BAI showed low inter-annual variability (**Fig. 4.8a**). Positive BAI trends of *F. sylvatica* and *Q. petraea* were explained by the increase in tree DBH (**Fig. 4.8b**). Climate variables explained the inter-annual BAI variability in the three studied species, the BAI decrease in *F. sylvatica* and part of the BAI decrease in *Q. petraea*. Finally, tree-to-tree competition explained most of the BAI decrease in *Q. petraea* and the BAI decrease observed in *Q. pyrenaica*.

Table 4.4. Regression coefficients of the fixed effects (standard errors are shown in parentheses), marginal (R^2_m) and conditional R^2 (R^2_c) for the best linear mixed-effects models of basal area increment for *F. sylvatica*, *Q. petraea* and *Q. pyrenaica*, considering the 1994–2015 period. Predictors were standardized previously to fit the models. Significance levels: ** $P < 0.01$ and ***$P < 0.001$, respectively. "×" indicates interactions.

	F. sylvatica	***Q. petraea***	***Q. pyrenaica***
Intercept	2.611 (0.073) ***	2.821 (0.094) ***	2.355 (0.115) ***
Annual DBH	0.275 (0.045) ***	0.265 (0.060) ***	
Annual BA		-0.298 (0.095) **	-0.453 (0.077) ***
Fraction of *F. sylvatica*		-0.299 (0.103) **	-0.464 (0.141) **
Fraction of *Q. petraea*			-0.366 (0.134) **
Fraction of *Q. pyrenaica*		-0.306 (0.108) **	-0.570 (0.151) ***
T_{March}	0.078 (0.016) ***		
P_{April}	0.064 (0.018) ***		
$P_{from\ previous\ June\ to\ previous\ October}$	0.077 (0.015) ***		
$T_{March} \times P_{April}$	-0.100 (0.027) ***		
$P_{from\ April\ to\ July}$		0.030 (0.007) ***	0.041 (0.008) ***
$P_{from\ previous\ July\ to\ previous\ September}$		0.037 (0.008) ***	
R^2_m	0.307	0.381	0.365
R^2_c	0.612	0.858	0.879

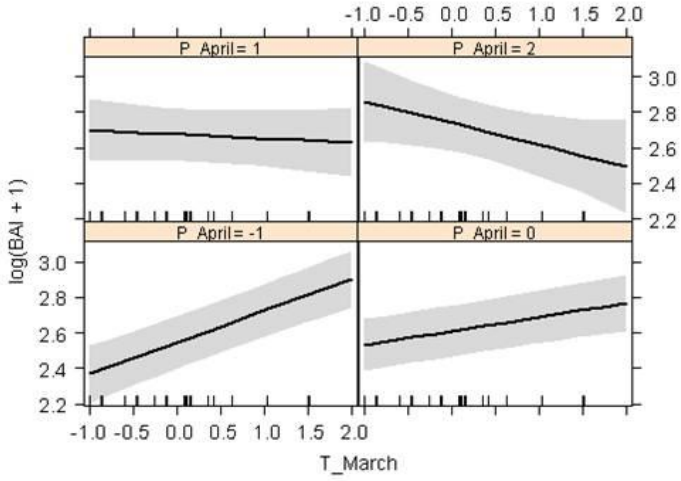

Figure 4.7. Effects of interactions between climate variables (P April, April precipitation; T_March, mean March temperature) on radial growth (BAI, basal area increment) of beech according to the selected linear mixed-effects model. Factors are standardized. Shaded bands indicate the 95% confidence intervals. Positions of the data along the abscissa axis are denoted by tick marks.

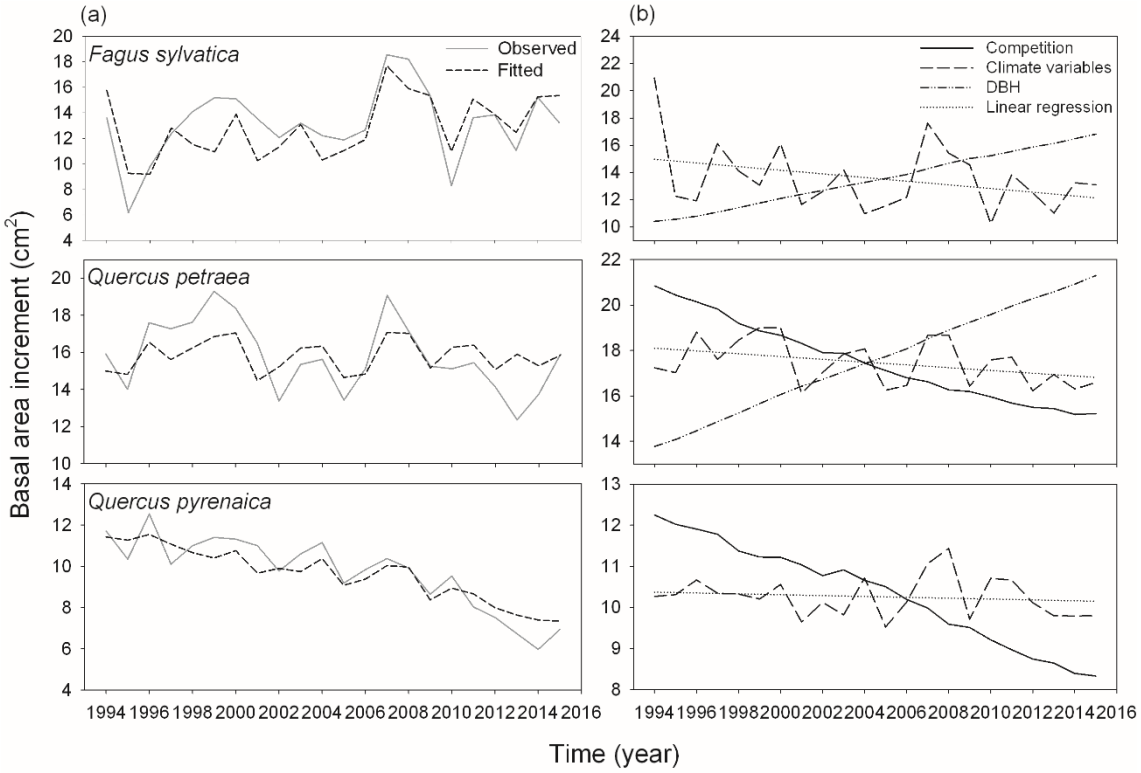

Figure 4.8. Observed and predicted basal area increment (BAI) for *Fagus sylvatica*, *Quercus petraea* and *Quercus pyrenaica* (a) and BAI prediction series for the variation, within the studied period, of tree diameter (DBH), competition (total BA and the fraction of it belonging to each of the species) and climatic effects separately, keeping the rest of the fixed effects constant (mean value of the period) (b). In the (*b*) plots, linear regressions were fitted to BAI predictions for the variation in climate variables (keeping DBH and BA constant) to show the long-term BAI trend but not considering annual variability.

4.4. Discussion

Contrary to expectations, we found that the increase in temperatures since the 1970s (**Fig. 4.2**) has not benefited the sub-Mediterranean *Q. pyrenaica* over the temperate species *Q. petraea* and *F. sylvatica*. According to our results (**Fig. 4.6**), the competitive dynamics benefited *Q. petraea* and especially *F. sylvatica*, the growth rates of which are increasing with respect to the other species although *Q. petraea* currently displays higher absolute growth (**Fig. 4.3**). This result can be partly explained by the increase in competition associated with the cessation of forest management, which has been a major factor behind the decline in growth of *Q. petraea* and *Q. pyrenaica*, i.e. they are being outcompeted by beech (**Fig. 4.8b**). This study reinforces the notion that the

reduction in logging and grazing has been one of the main drivers of forest dynamics in Spain over recent decades (Hernández et al. 2019).

4.4.1. Climate-growth relationships

Despite the higher vulnerability of beech to extreme climate events such as drought and frost in comparison to both *Quercus* species (Aranda et al. 1996, 2000, 2005), beech growth was the least sensitive to mean climate conditions (**Figs. 4.4** and **4.5** and **Table 4.2**). Unlike the findings of studies conducted in other temperate forests with Mediterranean influence (Piutti and Cescatti 1997; Rozas 2001) or those of previous studies focusing on aged trees of this forest (Dorado-Liñán et al. 2017a), high temperatures did not seem to be a limiting factor for beech growth. In fact, the only significant negative impact on growth that was identified occurred during the climate window Sep. 29 - Oct. 28 (**Figs. 4.4** and **Table 4.2**), when radial growth was negligible or stopped (Martinez del Castillo et al. 2018). Similarly, site conditions did not seem to be especially limiting to beech growth. While many missing rings were detected in dominant beeches in other temperate forests located further north due to adverse climate conditions or suppression caused by intense competition (Rubio-Cuadrado et al. 2018c), no missing rings were detected in this case. These results agree with those of other recent studies which point to adaptation to drought in the most southerly beech forests (Tegel et al. 2014; Cavin and Jump 2017; Muffler et al. 2020).

The influence of precipitation from June to October of the previous year on beech growth (see section 4.3.3 *Climate-growth relationships*) is related to the amount of carbohydrates stored in the previous growing season and therefore available at the beginning of the current vegetative period (Bréda et al. 2006), whereas the influence of March temperature could be related to earlier breaking of winter dormancy along with enhanced stimulation of the cambium activity (Seidling et al. 2012). In this respect, beeches in the study area sprout at the end of April (Millerón et al. 2012). It is also worthy of note that the beech trees in this study were not sensitive to June precipitation, which has been shown to drive growth in this species in populations of northern Spain (Rozas et al. 2015), while the precipitation just before and at the

beginning of the vegetative period was significant (**Table 4.2**). This may be explained by the fact that the phenology of these trees was more advanced in comparison to northern populations located in cool, wet sites. Finally, spring frosts cause noticeable growth losses in such populations (Dittmar et al. 2006). In the study area, four spring frosts have occurred in the last 25 years: 1995, 2010, 2013 and 2017 (data not shown). 1995 and 2017 were pointer years but sharp drops in the beech radial growth was found in all these years.

Radial growth of the two *Quercus* species was also related with the precipitation during the previous growing season, as well as with spring and summer precipitation of the growth year. In addition, the temperatures of June and July (see section 4.3.3 *Climate-growth relationships*), when the highest radial growth occurs (assessed through band dendrometer measurements not shown in this paper), and those from mid-March to mid-April (**Table 4.2**), just before the beginning of the vegetative period, were inversely related with the total growth of *Q. petraea* and *Q. pyrenaica*, respectively, which may be due to their higher proportion of living parenchyma in sapwood and higher respiration values per unit volume of living parenchyma compared with *F. sylvatica* (Rodríguez-Calcerrada et al. 2015).

4.4.2. Species competitive dynamics

The BAI trends (**Fig. 4.3**) and the competitive advantage series (**Fig. 4.6**) are clearly linked: the higher growth increments (i.e. the higher slope of the splines in **Fig. 4.3**) of *F. sylvatica* and *Q. petraea* compared with *Q. pyrenaica* until 1990 led to large positive values, around 20%, of $CA_{Fsyl\text{-}Qpyr}$ and $CA_{Qpet\text{-}Qpyr}$. From then on, there was a stabilization of *F. sylvatica* growth along with a decrease in growth in both *Quercus* species and consequently, $CA_{Fsyl\text{-}Qpet}$ and $CA_{Fsyl\text{-}Qpyr}$ continued to maintain positive values while $CA_{Qpet\text{-}Qpyr}$ alternated between positive and negative values although the positive values predominated due to the greater decreases in *Q. pyrenaica* growth. Finally, there was a sharp drop in $CA_{Fsyl\text{-}Qpet}$ and $CA_{Fsyl\text{-}Qpyr}$ due to damage suffered by beech in the late frost of 2017.

Most of the relationships between the competitive advantage series and climate (**Table 4.3**) can be explained by the different climate-growth relationships presented in **Fig. 4.4**, which are associated with differences in spatio-temporal use of water, cambium phenology (Michelot et al. 2012) and physiology (Aranda et al. 1996, 2005). While beech growth showed no relationship with precipitation from May to June, both *Quercus* species presented significant positive relationships. Thus the precipitation in these months benefits the *Quercus* species over *F. sylvatica*. Similarly, *Q. pyrenaica* growth showed no relationship with summer temperatures, whereas *Q. petraea* presented significant inverse relationships. Consequently, high summer temperatures, along with low precipitation in February and June, will have a negative impact on *Q. petraea* against *Q. pyrenaica*. High precipitation in February may benefit *Q. petraea* growth to a greater extent than *Q. pyrenaica* because its radial growth starts earlier, as in similar Iberian temperate forests (Pérez-de-Lis et al., 2017),

In our hypothesis, we expected an improvement in the competitive capacity of the more drought resistant species, as previously reported in temperate forests of northern Spain under mesic conditions (Rubio-Cuadrado et al. 2018b). However, in recent decades the competitive advantage series has shown a tendency favoring temperate species, especially beech, despite the negative impact on beech growth of extreme climate events such as droughts (Rubio-Cuadrado et al. 2018c) and spring frosts (Dittmar et al. 2006). These results may be related to the lower sensitivity and greater resistance to drought shown by rear-edge beech populations compared to those situated at the core of the species range (Cavin and Jump 2017; Serra-Maluquer et al. 2019). This greater resistance may be explained by favorable local environmental factors (e.g. site topography, soil water holding capacity) or by acclimation to drought (Rodriguez-Calcerrada et al. 2010) through phenotypic plasticity or genotypic adaptation. In any case, recent studies have revealed high resilience to drought in beech saplings, which rapidly resume physiological activity after the dry period (Pflug et al. 2018). These aspects clearly merit further investigation to determine whether adult beech trees display similar resilience to different extreme climate events (droughts, frosts) in rear-edge populations.

4.4.3. Factors influencing species growth trends

The model has been built for the period 1994-2015 as we do not know the precise evolution of the competition before the first forest inventory carried out in 1994. Although the time frame considered may be short, due to the relatively intensive use by cattle in the past and its subsequent abandonment, there has been a considerable increase in competition in this short period of time, which makes this forest an ideal site to study its effect on growth. The systematic sampling of trees performed, where all plots (of the inventory carried out in the studied forest in 2005) with mixed forest were sampled, and the high EPS values (**Table 4.1**) make our models representative of the growth dynamics of the dominant and co-dominant trees of the whole forest. However the short time frame considered together with low number of trees per species sampled limits the scope of the results. Further research studying longer periods of time and larger number of trees, and covering the distribution area of the species, are needed to know the factors that are influencing at a global level the growth trends of *F. sylvatica*, *Q. petraea* and *Q. pyrenaica*.

As reported in other studies (Monserud and Sterba 1996; Cescatti and Piutti 1998; Diaconu et al. 2015), most or at least a large proportion of the tree growth in *F. sylvatica* and *Q. petraea* was explained by tree size (DBH; **Table 4.4**). In alternative models for *Q. pyrenaica* that included the DBH (results not shown), this variable also explained most of the radial-growth variability, but was not significant because it had a very wide confidence interval. Both *Quercus* BAI models, especially the *Q. pyrenaica* model, were less sensitive to climate than the *F. sylvatica* model, as shown by the lower coefficients of the climate factors (**Table 4.4**), hence displayed lower inter-annual variability (**Fig. 4.8a**).

According to our BAI models (**Table 4.4**), the increase in competition following the cessation of forest management is the most important factor related with the negative growth trend of *Q. petraea* and *Q. pyrenaica*, although climate also explained some of the *Q. petraea* growth decline (**Figs. 4.3** and **4.8b**). These results are concordant with previous works, where high-frequency growth changes are related to climate, while radial growth is explained by the size and competition (Sánchez-

Salguero et al. 2015; Liang et al. 2019). Indeed, competition among trees may cause much larger reductions in forests growth and carbon uptake than climate stress (Vayreda et al. 2012; Rozas 2014). The greater importance of competition rather than climate in explaining tree radial growth has also been reported in large-scale studies conducted both in temperate-boreal (Foster et al. 2016) and in water-limited ecosystems (Gómez-Aparicio et al. 2011). However, some studies give greater weight to the climate and global warming effect on growth trends, especially in Mediterranean rear-edge forests (Piovesan et al. 2008; Dorado-Liñán et al. 2017b; Charru et al. 2017; Dorado-Liñán et al. 2019), although, these studies do not usually analyze the effect of the evolution of competition because it is uncommon that inventory data is available for a sufficiently long period of time. Our study shows the greater relative importance of competition in explaining radial growth not only in Mediterranean *Q. pyrenaica* but also in a rear-edge population of *Q. petraea*, providing further evidence of the complex relationships between climate and growth decline in some temperate forests at the equatorial range edge of their distribution (Tegel et al. 2014; Cavin and Jump 2017; Muffler et al. 2020). In fact, beech is currently expanding in Spain despite the reported aridification trends (Sánchez de Dios et al. 2016, 2020) due to its competitiveness, shade tolerance and greater dispersion capacity (Harmer 1994; Millerón et al. 2013), which allows it to access the best situations in terms of soil depth and orientation. The competition was not significant in the *F. sylvatica* BAI model (**Table 4.4**), possibly due to its greater competitiveness in comparison to the oak species (Hein and Dhôte 2006; Manso et al. 2015). This could result in a negative influence of beech admixture on oak. However, according to the models obtained, the presence of *Q. pyrenaica* seems to be the most limiting for the growth of both *Quercus*, while the presence of *Q. petraea* was the least limiting. This result may be influenced by the larger average size of *Q. pyrenaica* trees (see section 4.2.1 *Study area*) and the direct relationship between size and competition (Stadt et al. 2007). Furthermore, previous studies have shown that competition for resources in unfavorable climatic years may be lessened in mixed beech-oak stands with respect to pure stands (del Río et al. 2014).

Changes in tree-to-tree competition must be considered in order to understand long-term changes in growth and forest dynamics since they may be more relevant than climate to forecast changes in forest composition and dynamics (Sánchez-Salguero et al. 2015). In addition, changes in competition can drive or modulate the responses of tree growth and functioning (e.g., water-use efficiency) to climate (Linares et al. 2010; Martín-Benito et al. 2011; Fernández-de-Uña et al. 2015; González de Andrés et al. 2018). The effect on tree growth of the increase in competition resulting from the abandonment or change in previous forest management practices (which is common in many European forests) and that of global warming, can be difficult to unravel when analyzing the causes of growth decline. Therefore, by combining dendrochronological data with historical forest inventories it is possible to provide estimates on the evolution of stand competition among trees over time and improve our knowledge on the causes of growth decline in some of the temperate rear-edge forests.

4.5. Conclusions and management implications

There has been an increase in temperatures in the study area from 1975 onwards. However, the rear-edge *Q. petraea* and especially, *F. sylvatica* presented low sensitivity to climate and showed favorable evolution of their competitive capacity over the Mediterranean *Q. pyrenaica*. *F. sylvatica* also showed higher competitive capacity than *Q. petraea* throughout most of the studied period. Spring frosts, in the case of *F. sylvatica*, and increased competition resulting from the cessation of forest management, for the two *Quercus* species, were the most limiting factors to tree growth. Management strategies, such as selective thinning and promoting of sexual reproduction in *Q. pyrenaica* should be considered as means to improve long-term growth and enhance the resilience of *Quercus* populations.

4.6. References

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CAPÍTULO 5. DIFFERENTIAL RESPONSE OF OAK AND BEECH TO LATE FROST DAMAGE: AN INTEGRATED ANALYSIS FROM ORGAN TO FOREST

Este capítulo reproduce el texto del siguiente artículo ya publicado:

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Abstract

Intense spring freezing events can kill the recently produced cohort of leaves, forcing trees to expend additional carbon and nutrient stocks to produce a second cohort of leaves. The future trends in the frequency of late spring frosts will affect the adaptation of some tree species to their current habitats. Here we studied the effect of a late frost which occurred in 2017 on a mixed beech (*Fagus sylvatica*)-oak (*Quercus petraea*) forest located in central Spain, where these species reach their southernmost distribution limits. We followed a multi-scale approach from organ to forest levels. At the organ level, leaf and stem morphological and biochemical traits were compared between frost-damaged and non-damaged trees. At the tree level, we compared the 2017 radial growth between damaged and non-damaged trees. At the stand level, the 2017 Leaf Area Index (LAI) and daily variations of NDVI during 2017 were compared with those of average years in areas dominated by beech and oak. Finally, at the forest scale, daily NDVI dynamics during 2017 were compared with those of the three previous years. According to our results, beech trees damaged by late frost kept non-structural carbohydrate (NSC) concentrations stable by drastically reducing wood production. This growth reduction could compensate for the drop in carbon inputs due to the death of the first leaf cohort, the need to form a second leaf cohort, the one-month delay between both leaf flushes and the smaller photosynthetic surface of the second leaf cohort. In contrast, although the frost-damaged oaks lost the first cohort of leaves and formed a second one, no differences in leaf individual area and phenology, nor stem NSC concentrations and radial growth were found when comparing damaged and non-damaged oaks. The differential response between both tree species seems to provide oak with a competitive advantage over beech.

5.1. Introduction

The ongoing climate change is negatively affecting forest health worldwide (Allen et al., 2010), and will likely alter species distribution over this century (Benito Garzón et

al., 2011; Hernández et al., 2017). Climate models predict a rising trend of climate warming at a planetary scale; this trend will be accompanied by an increase in climate variability, including an increase in the occurrence and severity of climate extremes such as frosts (Meehl et al., 2007). Winter warming has been linked to an advanced leaf-out in some deciduous tree species (Menzel, 2000; Menzel et al., 2003; Vitasse et al., 2018). This can extend the growing season of winter-deciduous species, but can also increase the chances of spring freezing events (Gazol et al., 2019; Richardson et al., 2018). While adaptation of winter-deciduous tree species to freezing temperatures has coupled leaf-out to minimum temperatures (Lenz et al., 2013; Vitasse et al., 2018), it is relatively common that expanding leaves and flowers get damaged by spring freezing events (Augspurger, 2013, 2009; Hufkens et al., 2012). Since the pioneering study of Cannell (1985) analyzing the risks of tree frost damage in Britain, there has been no consensus on whether climate change will decrease (Dai et al., 2013; Hänninen, 2016; Menzel et al., 2003; Morin and Chuine, 2014; Scheifinger et al., 2003) or increase (Abbas et al., 2017; Augspurger, 2013; Bigler and Bugmann, 2018; Gu et al., 2008; Hänninen, 2016; Inouye, 2008; Kramer, 1994; Vitasse et al., 2014b) the risk of late frost damage.

Leaf damage by spring freezing has a penalty to the tree. If the intensity and/or duration of the freezing event are moderate and do not kill the leaves, their morphology, physiology and chemical composition will be altered during most or all of their life span (Klosson and Krause, 1981a, 1981b; Sakai and Larcher, 1987). However, intense and/or long freezing events can kill the recently produced cohort of leaves, forcing the trees to flush a second cohort of leaves. Because the initial growth of spring shoots in winter-deciduous trees is sustained by carbon reserves stored in woody tissues (Hoch et al., 2003), trees have to re-mobilize a new supply of non-structural carbohydrates (NSC) and mineral nutrients to produce this new cohort. Frost impact on the NSC pools will depend on the amount of new leaves produced, their capacity to assimilate CO_2, and the extent to which carbon sinks (e.g., meristems) are down-regulated or carbon-limited after the freezing event.

Studies on temperate forests have reported abrupt declines in leaf area index (LAI) the year on which spring frost occurs, relative to a year with no leaf affection by

freezing (Awaya et al., 2009). Because of this, the sapwood area potentially supplying water to a given leaf area (i.e. the Huber value; Huber, 1928) can increase relative to years with no freezing damage or relative to non-damaged trees. If the fewer new leaves benefit from having a delayed senescence (Zohner et al., 2018), higher nitrogen concentration, higher water supply, and thus higher rates of photosynthesis (Hoogesteger and Karlsson, 1992; Reich et al., 1999), the impact of reduced LAI on carbon gain at the tree or stand scales can be partly compensated. Wood production will also be likely affected by spring frosts (Hufkens et al., 2012). Altered hormonal signaling caused by reduced foliage and/or reduced carbon availability caused by the extra use of NSCs on resprouting can reduce stem growth (Buttò et al., 2020). Besides ring width, wood density can decrease after freezing damage to leaves, affecting the water storage capacity of stem sapwood (Vannoppen et al., 2018). There is therefore a coupling between carbon storage (e.g. NSC pools), carbon sources (e.g. leaf area), hydraulic conductivity (e.g. sapwood water conducting area) and carbon sinks (e.g. radial growth) that can differently extend to tree, stand and forest scales depending on species frost resilience.

The impact of leaf freezing on tree physiology scales-up to ecosystem processes, sometimes leading to a reduction in gross and net primary production (Awaya et al., 2009; Hufkens et al., 2012), due mainly to canopy recovery processes that can take several months (Nolè et al., 2018). Spectral indices derived from satellite images provide useful information on the consequences of spring freezing events on ecosystem functional traits, such as the reduction of canopy leaf area and primary productivity, or the duration of the freezing stress effects (Bascietto et al., 2018; Greco et al., 2018; Nolè et al., 2018). There is a need to combine information obtained at different spatial scales to study the impact of frost and the post-frost resilience at the organ, tree, stand, and forest scales. Despite its potential to understand the impact of freezing on forest stands, few studies have integrated information at different scales.

European beech (*Fagus sylvatica* L.) and sessile oak (*Quercus petraea* [Matt.] Liebl.) are co-occurring and widespread temperate tree species in central Europe. Since the last glaciation, European beech has expanded over Spain, often replacing sessile oak forests, a process that continues today (Gómez et al., 2019; Perea et al.,

2020; Sánchez de Dios et al., 2016). Both species reach their southernmost limits of distribution at the studied forest ("El Hayedo de Montejo", central Spain) (Pardo et al., 2004). This forest has a continental Mediterranean climate, with relatively frequent years in which leaves of a considerable number of trees are visibly damaged by late frosts (hereafter spring frosts; four in the last 25 years). If spring frost frequency and, thus, tree damage increases due to climate change, the vigor of these beech-oak populations may be compromised. An extraordinarily warm winter to early-spring period in 2017 caused the premature leaf out of these species in the "El Hayedo de Montejo" forest. A spring frost occurring over two consecutive nights in late April 2017, reaching -4.6 °C, was enough to scorch the developing shoots of many beech and sessile oak trees (**Figs. 5.1** and **5.2**); in our research, we followed a multiscale approach to study its effects from organ to forest levels (**Table 5.1**). At the organ level, functional traits related with tree water transport and carbon balance were compared between trees damaged and non-damaged by the frost. At the tree level, we compared the 2017 radial growth between these two groups of trees. At the stand level, we analyzed the spring frost impact on LAI and Normalized Difference Vegetation Index (NDVI), distinguishing in both analyses between areas dominated by beech and oak. At the forest scale, the frost effect on NDVI was studied. We hypothesized that (i) the frost negative impact on carbon stocks, due to leaf scorching and the NSC expense to produce a second leaf cohort, would be buffered as a consequence of a decline in radial growth; (ii) LAI would be lower in 2017, due to a lower tree crown density and leaf size of the second leaf cohort and that, for these reasons, (iii) NDVI of 2017 would reach a lower and delayed maximum with respect to an average year.

5.2. Material and Methods

5.2.1. Study site

The study site, "El Hayedo de Montejo", is a mixed forest of 125 ha located at "Sistema Central" mountain range, central Spain (41° 07' N; 3° 30' W), between 1,250-1,500 m a.s.l. The dominant species are *Quercus pyrenaica* Willd., *Fagus sylvatica* L. (hereafter beech) and *Quercus petraea* (Matt.) Liebl. (hereafter oak), with relative basal areas of

50%, 27% and 23%, respectively. This study focused on beech and oak; it did not include *Quercus pyrenaica* because its late phenology prevented the occurrence of extensive damages in trees of this species. During centuries of firewood and cattle grazing use, the forest had an open woodland structure of dispersed old and large trees, and scarce tree recruitment (Pardo and Gil, 2005). However, cattle grazing was forbidden in 1961 and the last logging took place in 1962 (Gil et al., 2009; López Santalla et al., 2003), which has favored the increase of tree density in the last decades.

Climate data were obtained from a meteorological station located in the study forest and managed by the "Natural Systems and Forest History" research group of "Universidad Politécnica de Madrid", Spain. The climate is continental subMediterranean, with 900 mm of mean annual rainfall and a prolonged dry period during July and August. The mean annual temperature is 9.5 ºC and temperatures below 0º C can occur from November to February. In the last 25 years there were spring frosts damaging the trees in 1995, 2010, 2013 and 2017. The soil has been classified as humic cambisol (Pardo et al., 1997) and the horizon A reaches 50 cm of depth on average, enabling relatively high water storage during dry periods.

5.2.2. Frost event

In April 2017, few days after leaf-out in both species, there was an abrupt fall in temperature during two consecutive nights; between April 26 and 28, temperatures reached a negative peak of -4.6 °C (**Fig. 5.1a**), killing the leaves of trees with advanced phenology (**Fig. 5.2**). Most of the trees were damaged by the spring frost (see more details in the section 5.2.5 *Tree level*). Only the trees or branches that had not sprouted yet, showed no frost damage.

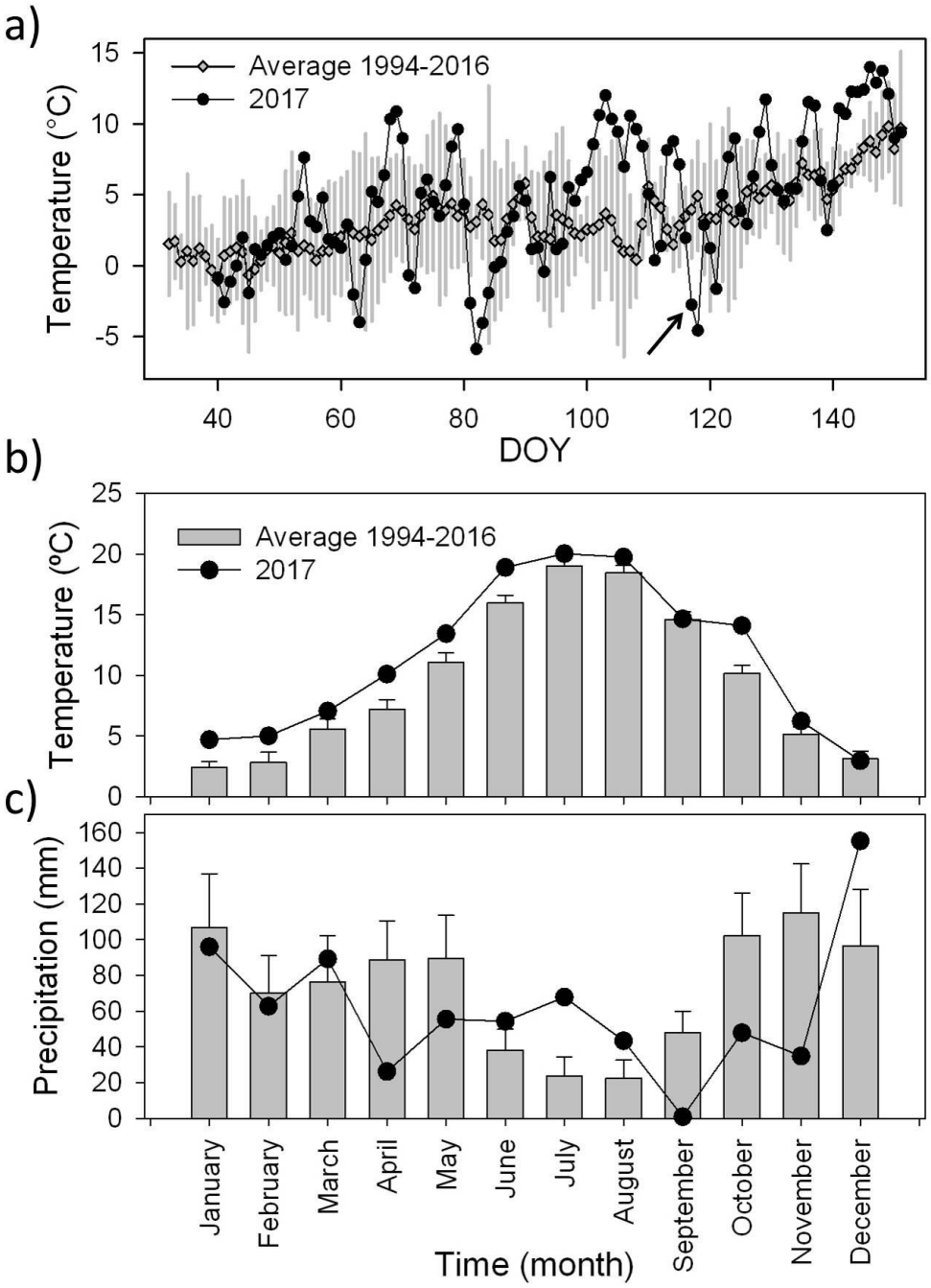

Figure 5.1. Daily minimum air temperatures from February to May (a), average monthly temperatures (b) and total monthly precipitations (c) in 2017 compared with an average year for the 1994-2016 period. Vertical gray lines (a) and error bars (b and c) indicate 95% confidence interval. The arrow in the top panel points to the first day of the late frost. DOY stands for Julian day of the year.

Figure 5.2. Damages produced by a late frost in beeches and oaks in the study area ("El Hayedo de Montejo") located in central Spain. Inset shows scorched leaves in a beech tree.

5.2.3. Bud and leaf phenology

The overall leaf phenology of the forest was monitored weekly by the same observer during the spring of 2017, distinguishing between trees damaged and non-damaged by the frost. The number of trees on which phenology was measured after the spring frost was variable, with a minimum of 10 trees by measuring date (5 damaged and 5 non-damaged) for each species. The pre-frost phenology, i.e., the date when peaked the bud opening of the first cohort of leaves in 2017, was obtained from general observations of the beech stands on routine weekly observations during the first months of 2017. It should be noted that those trees that had not sprouted when the frost occur delayed their bud opening as consequence of this frost. Four phenophases were considered: closed bud, bud opening and leaf elongation, extended leaves, and complete development of the leaves (expanded and hardened) following Millerón et al. (2012). A tree was included in a phenophase when more than 50% of its crown belonged to the same phase, and a given phenophase was assigned to the forest when more than 50% of the trees were in that phase. These data were compared with the phenology of a typical year characterized by a detailed inventory of data performed

weekly in ten beech trees and eight oak individuals during six consecutive vegetative periods from 2006 to 2011 (Millerón et al., 2012).

5.2.4. Organ level

To estimate the frost effect on morphological and biochemical traits, we sampled the main-stem xylem, annual twigs and leaves in 10 adult beeches and 10 adult oaks (**Table 5.1**). Half of these trees (5 beeches and 5 oaks) had not been damaged by the spring frost (0% of the crown damaged) and the other half had been severely damaged (>90% of the crown damaged). The trees were selected from representative locations in the forest in terms of slope, orientation and basal area, which is 28.8 m^2 ha^{-1} on average. The beech and oak trees sampled were located in homogeneous areas inside beech- and oak-dominated stands within a circular surface of 100 and 150 meters in diameter, respectively.

Stem xylem was sampled at the base of the trees using a Pressler increment borer at the following dates: May 8th, ten days after the frost event; June 1st, when non-damaged beech trees finished spreading the leaves; June 23rd, when damaged beech trees finished spreading the leaves of the new, second leaf cohort; July 24th, in the middle of the vegetative period; September 28th, near the end of the vegetative period but without trees showing yellowing leaves yet; December 22nd, during the dormant period. We extracted one 3-cm-long core per tree and date. After the extraction, bark and phloem were removed from the stem segments; the stem xylem was immediately placed in a Styrofoam box with ice to transport the samples to the laboratory, where they were stored at -80 °C.

Table 5.1. Summary of the multiscale analysis performed.

Multiscale analysis				
Level	Organ	Tree	Stand	Forest
Aim	Study frost effect on morphological and biochemical traits	Study frost effect on tree growth and growth phenology over time	Study frost effect on tree canopy	Study frost effect on forest canopy
Sampling	Main-stem xylem, annual twigs and leaves in 10 beech and 10 oak trees	Radial growth in 63 beech trees and 8 oak trees	– Ground-based LAI in 17 beech-dominated points and 18 oak-dominated points – NDVI dynamics in beech- and oak-dominated stands	Forest NDVI dynamics
Time scale	– A single sampling of annual twigs and leaves in 2017 – 6 samplings of stem xylem over 2017	8 measurements per tree and year over 2017 and 2018	– A single sampling of LAI in 2015 and 2017 – NDVI was analyzed between 2014 and 2017 with daily resolution	NDVI was analyzed between 2014 and 2017 with daily resolution
Statistical analyses	Mann-Whitney *U* tests comparing damaged and non-damaged trees	– Growth modeling by fitting a sigmoid function to 2017 growth for each tree – Mann-Whitney *U* tests comparing damaged and non-damaged trees	– Mann-Whitney *U* tests comparing LAI values in 2015 and 2017 for each species – Kolmogorov-Smirnov test comparing average NDVI annual series for the 2014-2016 period and 2017 NDVI series for each species	Kolmogorov-Smirnov test comparing average NDVI annual series for the 2014-2016 period and 2017 NDVI series for the whole forest

We collected two annual twigs with leaves per tree with a 6-meter pole on September 28th. Due to the height of the trees, we could only sample twigs and leaves in 6 beech and 6 oak trees (4 damaged and 2 non-damaged by the frost in both species). These samples were also preserved in the Styrofoam box with ice for transportation. In the laboratory, fresh leaves were scanned (Epson Expression 10000XL, Suwa, Japan) to measure leaf area, using the software WinFOLIA (Regent Instruments Inc., Canada). The base of the twig was debarked and measured with a precision electronic caliper to obtain the sapwood section and calculate the Huber value (i.e. ratio between sapwood area and distal leaf area; cf. Huber, 1928). The length of the apical bud was measured with an electronic caliper. Finally, the leaves were dried at 60 °C during 72 h to obtain the dry weight, using a precision balance

(OHAUS AR 2140, Pine Brook, New Jersey, USA), and the leaf mass per area (LMA; the ratio between dry weight and leaf area).

The chemical analyses of nitrogen (N) and non-structural carbohydrate (NSC) concentrations on stem sapwood and leaf samples were performed following Palacio et al. (2012). First, all samples were dried at 60 °C for 72 h and were milled to a fine powder in a ball mill (Retsch Mixer MM301, Leeds, UK). Total carbon (C) and N mass-based concentrations were analyzed in leaves with an elemental analyzer (Elementar VarioMAX N/CM, Hanau, Germany). Soluble sugars (SS) were extracted with 80% (v/v) ethanol and their concentration determined colorimetrically, using the phenol–sulphuric method of Dubois et al. (1956) as modified by Buysse and Merckx (1993). Starch and complex sugars remaining in the undissolved pellet after ethanol extractions were enzymatically reduced to glucose. NSCs measured after ethanol extraction are referred to as SS, whereas NSCs measured after enzymatic digestion are referred to as starch. Both are expressed in glucose equivalents. The sum of SS and starch is referred to as total NSCs.

The differences between groups (trees damaged vs. non-damaged by the frost) for organ-level variables were analyzed for each species with Mann-Whitney *U* tests (**Table 5.1**). In the twig variables the data were previously averaged per tree to avoid pseudo-replication error (Hurlbert, 1984). We calculated the relative differences between groups for twig and leaf traits (eq. 1):

$$\text{Relative difference} = |(D - ND) / ((D + ND) / 2)| \quad (1)$$

where *D* and *ND* are the average values for damaged and non-damaged trees, respectively.

We also analyzed the temporal variation of the stem xylem traits, through the rate of change (eq. 2):

$$RC_t = (S_t - S_{t-1}) / S_{t-1} \quad (2)$$

where RC_t is the rate of change at time *t* and S_t and S_{t-1} are a stem xylem variable at time *t* and *t-1*, respectively.

5.2.5. Tree level

Since 2015 there are dendrometer bands (DB 20, EMS Brno) placed on 71 beech trees and 8 oak trees in the study forest (**Table 5.1**). The dendrometers were placed at 1.3 m directly over bark on beech trees. In the oaks, the outermost dead bark was previously smoothed and removed to avoid stem deformities. These 79 trees were classified according to the frost damage suffered in 2017: <25%, 25-50% and >50% of the crown damaged. Measurements to the nearest 0.1 mm were acquired at variable time intervals during the year depending on the growth rate (average time interval during the growing season was 22 days). All measurements were acquired in the morning to avoid diurnal bias caused by stem shrinkage from transpiration (Sheil, 2003). Girth increment data were transformed to radial increments assuming a cylindrical tree shape. The basal area increments (BAI) and the basal area (BA, i.e. accumulated BAI) were calculated for each tree as:

$$BAI_t = \pi(r_t^2 - r_{t-1}^2) \quad (3)$$

$$BA_{yt} = \sum_{i=0}^{n} BAI_i \quad (4)$$

where BAI_t is the basal area increment at time t, r_t and $r_{t\text{-}1}$ are the stem radius at times t and t-1, respectively, BA_{yt} is the basal area in the year y at time t, and n is the number of basal area increments measured in the year y until the time t.

For this study we used growth data of 63 beech trees, 12 of them having <25% of the crown damaged (hereafter non-damaged) and 51 having >50% of the crown damaged (hereafter damaged), leaving out those trees with intermediate crown damage (25-50%). Given the low number of monitored oaks (8), these were grouped in non-damaged (<50% of the crown damaged in this case; 2 trees) and damaged (>50% of the crown damaged; 6 trees). Based on these data, 72% and 80% of our sample of beech and oak, respectively, showed more than 50% of the crown damaged by the frost.

We modeled the growth of each tree over 2017 to estimate the day of year (DOY) when radial growth starts and ends ($DOY_{beginning}$ and DOY_{end}, respectively), the length of the active growth period (DOY_{end} - $DOY_{beginning}$) and the time at which the maximum growth rate occurs. A sigmoid function was fitted to the 2017 growth of each tree by nonlinear least squares using the *nls* function in R statistical software (R Development Core Team, 2017):

$$BAS = a / (1 + e^{(-b * (DOY - c))}) \quad (5)$$

where *BAS* is the standardized basal area according to the equation 6, with values from 0 to 1, and *a*, *b, c* are the model parameters, different for each tree, being *c* the DOY with maximum growth rate.

$$BAS_{it} = (BA_{it} - \min(BA_i)) / \max(BA_{it} - \min(BA_i)) \quad (6)$$

where BAS_{it} and BA_{it} are the standardized basal area and the basal area, respectively, for tree *i* at time *t*. Because the model estimated the start and end of growth asymptotically, we defined the start and the end of the active growth period as the day when *BAS* was 10% and 90% of the annual maximum (Moore et al., 2006).

We tested the differences in BAI and growth-related phenological variables between damaged and non-damaged trees with Mann-Whitney *U* tests.

5.2.6. Stand and forest level

To study the frost effects at the stand level (**Table 5.1**), we compared Leaf Area Index (LAI) values measured in July 2015 (a year without freezing damage) and in July 2017, when the leaf development is maximum. LAI values in 2015 were retrieved from a field inventory with ForeStereo, a device that acquires stereoscopic hemispherical image pairs and enables estimation of basal area among other variables (Rodríguez-García et al., 2014; Sánchez-González et al., 2016). Ground-based LAI can be obtained from the hemispheric images through the Poisson gap frequency model with slope correction (Montes et al., 2007). In 2015, a total of 125 inventory points were measured on the

nodes of a systematic 100 m × 100 m grid covering the entire forest area. For our current analysis, we selected points where one of the target tree species (beech and oak) dominates (>50% of the relative basal area): 17 beech-dominated points and 18 oak-dominated points. In 2017, the ForeStereo inventory was repeated in those points. Differences between LAI values in 2015 and 2017 were analyzed for each species with Mann-Whitney *U* tests.

Remotely sensed data acquired daily by the Moderate Resolution Imaging Spectroradiometer (MODIS) sensor and at 8-16 days frequency by Landsat sensors (Operational Land Imager—OLI, and Enhanced Thematic Mapper Plus—ETM+) were fused in accordance with Gao et al. (2015, 2006) (**Fig. 5.3**), obtaining synthetic daily data with 30 m of spatial resolution between 6th of March 2014 and 12th of January 2018 (see **Appendix A** of the Supplementary material). Areas dominated by beech or oak were defined as irregular polygons considering a recent land cover cartography (Gómez et al., 2019) and assuring they encompassed beech or oak plots as mentioned above. Values of the entire forest NDVI series and those from the beech and oak polygons were extracted and analyzed with TIMESAT software (Eklundh and Jönsson, 2017). Savitsky-Golay, Gaussian, and double logistic functions (Eklundh and Jönsson, 2017) were fitted to NDVI series at the stand and entire forest scales. The start- and end-of-season parameters were determined based on seasonal amplitude, defined as the difference between the base and maximum NDVI values for each individual season. The start occurs when the left part of the fitted curve reaches 0.5 of the amplitude value, counted from the base level, and the end of season is defined similarly but for the right side of the curve. Parameters of the phenological season characterizing the start, end, and length of the vegetative period, as well as the annual maximum NDVI and time of maximum NDVI were obtained. We tested the differences between average NDVI annual series for the 2014-2016 period and 2017 NDVI series, both for each stand (dominated by beech or oak) and for the entire forest, using two-sample Kolmogorov-Smirnov test. We also tested the possible zonal affection of the frost, and analyzed the NDVI data by altitude, obtaining seasonality parameters for 8 altitudinal ranges.

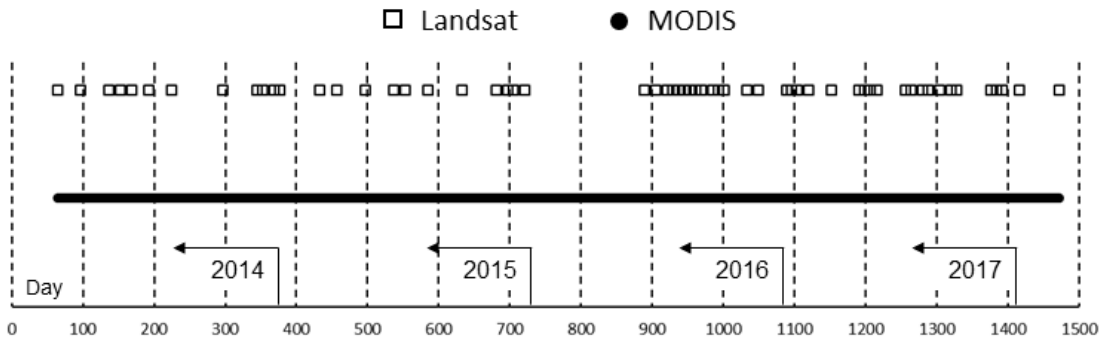

Figure 5.3. Distribution of the time instants when the Landsat and MODIS images employed were acquired.

5.3. Results

5.3.1. Bud and leaf phenology

In 2017, bud opening in part of the beech trees and oaks started approximately two weeks earlier than usual based on the 2006-2011 phenology (**Fig. 5.4**). Those trees were damaged by the freezing event, losing all open buds and leaves. The non-damaged beech trees sprouted three weeks later (during the second week of May) and the non-damaged oak trees five weeks later (during the last week of May) than damaged trees, considerably later than usual. The second cohort of leaves of the damaged beech and oak trees sprouted five weeks after the first cohort of leaves was damaged (during the last week of May). Thereafter, the phenology was similar in all oaks, damaged and non-damaged, whereas the damaged beech trees exhibited a delay in the phenophases when compared to those not damaged. For both species, the phenological phases occurred later than in an average year.

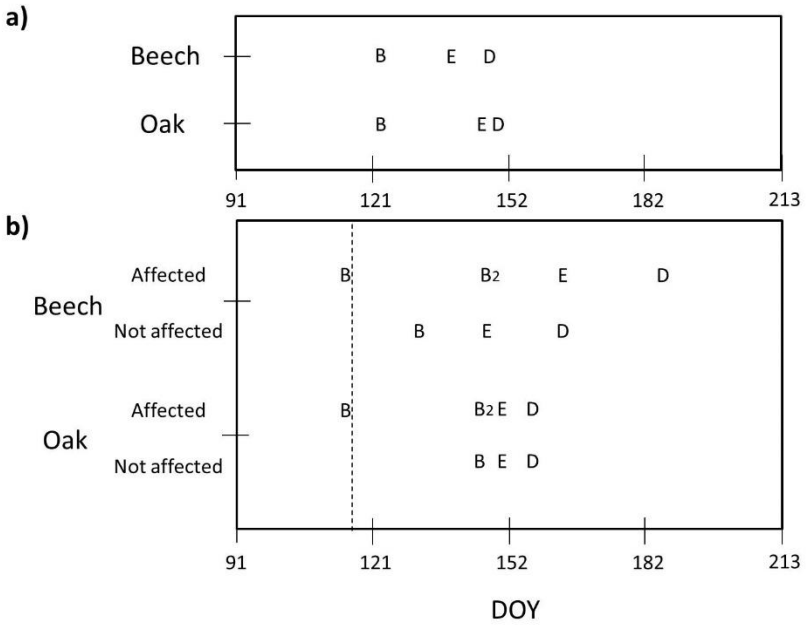

Figure 5.4. Chronogram of average leaf emergence time in beech and oak (period 2006-2011) (a) compared with the late-frost year 2017 (b). Legend: *B*, bud opening and unfolding of the first leaf cohort; B_2, bud opening and unfolding of the second leaf cohort; *E*, extended leaves; *D*, complete leaf development. For 2017, data are given for damaged and non-damaged trees separately. The spring frost is highlighted with a dashed vertical line. The abbreviation "DOY" stands for Julian day of the year.

5.3.2. Organ level: leaves and stems

Due to the small number of twig and leaf samples collected, the confidence intervals of the statistical analyses were large (**Table 5.2**). Differences at $p < 0.1$ between damaged and non-damaged beech trees were detected in almost all leaf-related variables. Leaves of damaged beech trees were lighter, smaller and had lower LMA and NSC concentrations but higher N concentrations than leaves of non-damaged beech trees. Differences between damaged and non-damaged oaks were similar, but smaller and not significant. In this respect, the average relative difference between damaged and non-damaged oaks for leaf and twig traits was 0.15 compared to 0.30 for beeches (see **Table 5.B1** in **Appendix B** of the Supplementary material). Oak leaves only presented differences at $p < 0.1$ in C concentrations. With respect to stem xylem NSCs, only beech trees showed significant differences between damaged and non-damaged trees, and these were only found for SS concentrations at the beginning and at the end of the

vegetative period (**Fig. 5.5**). On June 1st (DOY 152), when damaged beech trees were opening the buds and unfolding the leaves of the second leaf cohort and non-damaged beech trees were finishing spreading the leaves of the first leaf cohort, damaged trees exhibited higher SS concentration. This difference was caused by a decrease in SS concentration in non-damaged beeches, which was later compensated by a similar decrease in damaged trees (see rate of change values in **Fig. 5.5**). On the contrary, on September 28th (DOY 271), near the end of the vegetative period, damaged trees exhibited lower SS concentration than non-damaged trees. Differences in SS and NSC disappeared at the end of the year (on December 22nd, DOY 356), due to an increase in SS in damaged trees and a decrease in NSC in non-damaged trees.

Table 5.2. Mean (and standard deviation) of leaf and twig functional traits for beech and oak measured at the end of the vegetative period of 2017. "•" indicates differences at $p < 0.1$ between trees damaged and non-damaged by the frost. LMA is leaf mass per area, SS is soluble sugars, NSC is non-structural carbohydrates, N is nitrogen and C is total carbon expressed in % of dry mass.

	Beech		Oak	
Variable	**Damaged**	**Non-damaged**	**Damaged**	**Non-damaged**
Individual leaf dry weight (g)	0.05 (0.01) •	0.10 (0.01) •	0.33 (0.19)	0.50 (0.20)
Individual leaf area (cm^2)	13.22 (1.44) •	21.14 (0.95) •	45.40 (23.80)	71.10 (22.55)
LMA ($g\ m^{-2}$)	38.08 (4.09) •	45.86 (2.94) •	69.82 (7.99)	70.19 (6.19)
Dry leaf weight per twig (g)	0.27 (0.03) •	0.46 (0.02) •	2.04 (1.69)	2.64 (0.92)
Total leaf area per twig (cm^2)	70.52 (5.43) •	100.73 (2.28) •	289.22 (228.00)	372.25 (97.76)
Number of leaves per twig	5.35 (0.27)	4.77 (0.32)	5.95 (1.54)	5.28 (0.30)
Sapwood diameter of the annual stems (mm)	1.23 (0.19)	1.42 (0.05)	2.36 (0.75)	2.47 (1.01)
Huber value (10^{-4})	1.72 (0.47)	1.58 (0.09)	1.74 (0.51)	1.30 (0.71)
Average length of the apical buds (mm)	15.43 (1.69)	14.99 (0.28)	5.97 (0.72)	5.98 (0.25)
SS in leaves (%)	4.17 (0.55) •	6.06 (0.77) •	5.87 (1.11)	6.32 (0.30)
Starch in leaves (%)	2.88 (0.31) •	3.96 (0.54) •	5.76 (1.23)	6.35 (0.03)
NSC in leaves (%)	7.05 (0.84) •	10.02 (0.22) •	11.64 (2.22)	12.67 (0.27)
N in leaves (%)	2.40 (0.10) •	1.57 (0.02) •	1.95 (0.21)	2.07 (0.18)
C in leaves (%)	47.85 (0.69)	48.70 (0.07)	47.90 (0.34) •	46.84 (0.35) •
C/N ratio in leaves	19.95 (0.89) •	31.05 (0.36) •	24.83 (2.63)	22.74 (1.81)

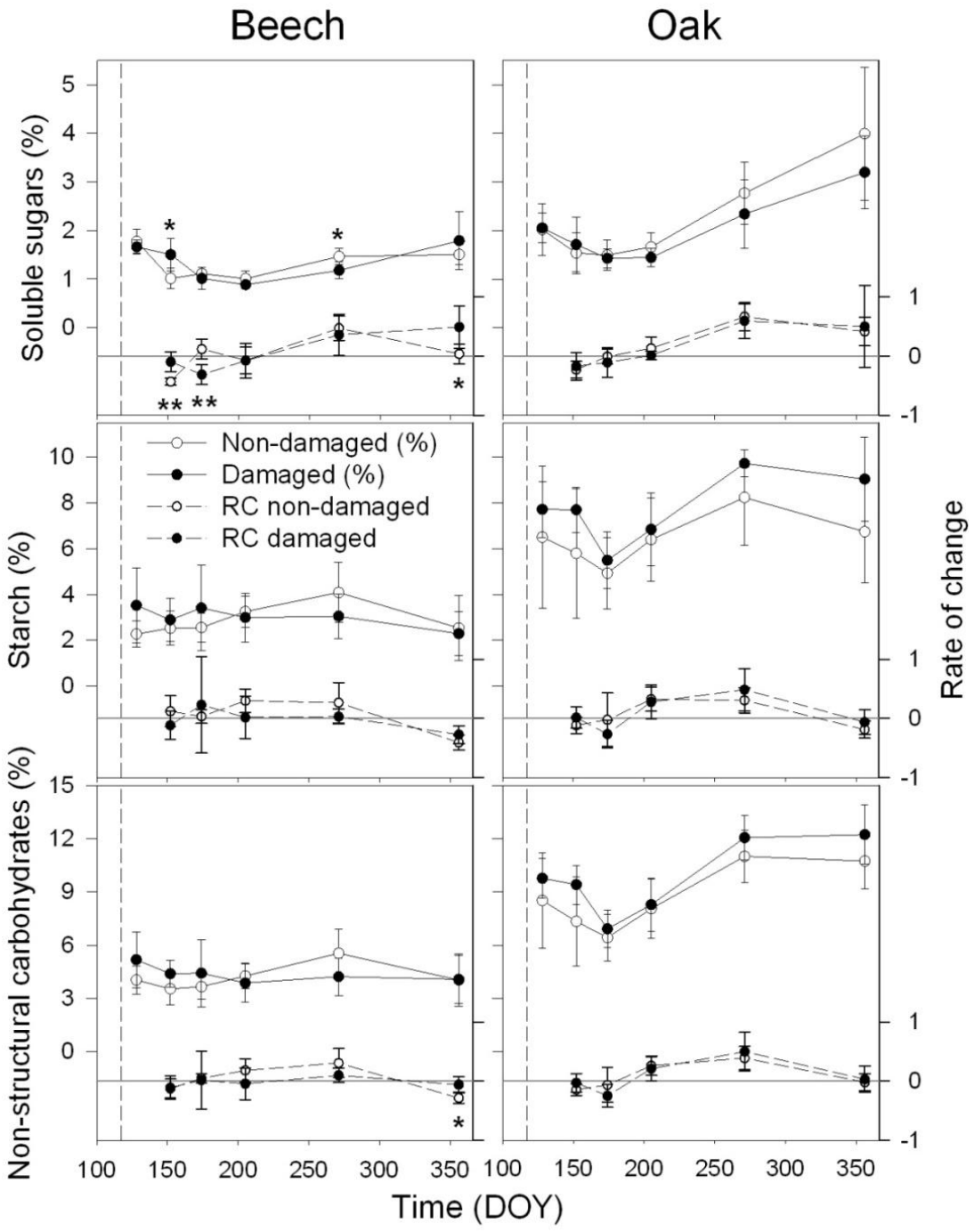

Figure 5.5. Concentrations, as percentage of dry matter (solid lines; left y-axis), and rates of change (RC) of the concentrations (dashed lines; right y-axis) of soluble sugars, starch and non-structural carbohydrates in stem sapwood of beech and oak trees, either damaged or not damaged by a late frost, throughout 2017. Data are means (± standard deviation bars). Asterisks indicate significant differences (*p < 0.05, **p < 0.01) for the same date. The spring frost is highlighted with dashed vertical lines. The abbreviation "DOY" stands for Julian day of the year. See equation 2 for definition of RC.

5.3.3. Tree level: radial growth

Damaged and non-damaged beech trees showed highly significant differences in radial growth throughout the study period, except at the beginning of the vegetative period (**Fig. 5.6**). On the contrary, both groups of oaks only showed differences at $p < 0.1$, and these were found only at the beginning of the growing season. The 2017 frost also influenced the radial growth of beech in 2018 (**Fig. 5.C.1** in **Appendix C** of the Supplementary material). In this year, the beech trees damaged by the 2017 frost had a significantly ($p < 0.001$) lower growth than those not damaged (9.0 vs. 14.9 cm^2 $year^{-1}$, respectively). On the contrary, oak growth in 2018 was not influenced by the 2017 frost ($p = 1$); the basal area increments of damaged and non-damaged oaks in 2018 were 5.6 and 6.2 cm^2 $year^{-1}$, respectively.

There were no significant differences between damaged and non-damaged trees in the estimated timing of maximum growth rate and growth end, nor in the length of the growth period of either species, but we found significant differences in the estimated growth start DOY for beech trees (**Table 5.3**). All phenological variables related with beech radial growth had higher variability in the group of trees suffering frost damage (**Fig. 5.C.2** in **Appendix C** of the Supplementary material). In this regard, 15.7% of the damaged beech trees did not grow at all, 11.8% grew for a period equal to or less than one month, and 35% grew for a longer period than any of the beech trees not damaged by the frost. However, all non-damaged beech trees grew for more than one month. It must be noted that these estimates are potentially affected by the stem swelling and deflation associated to dendrometer data.

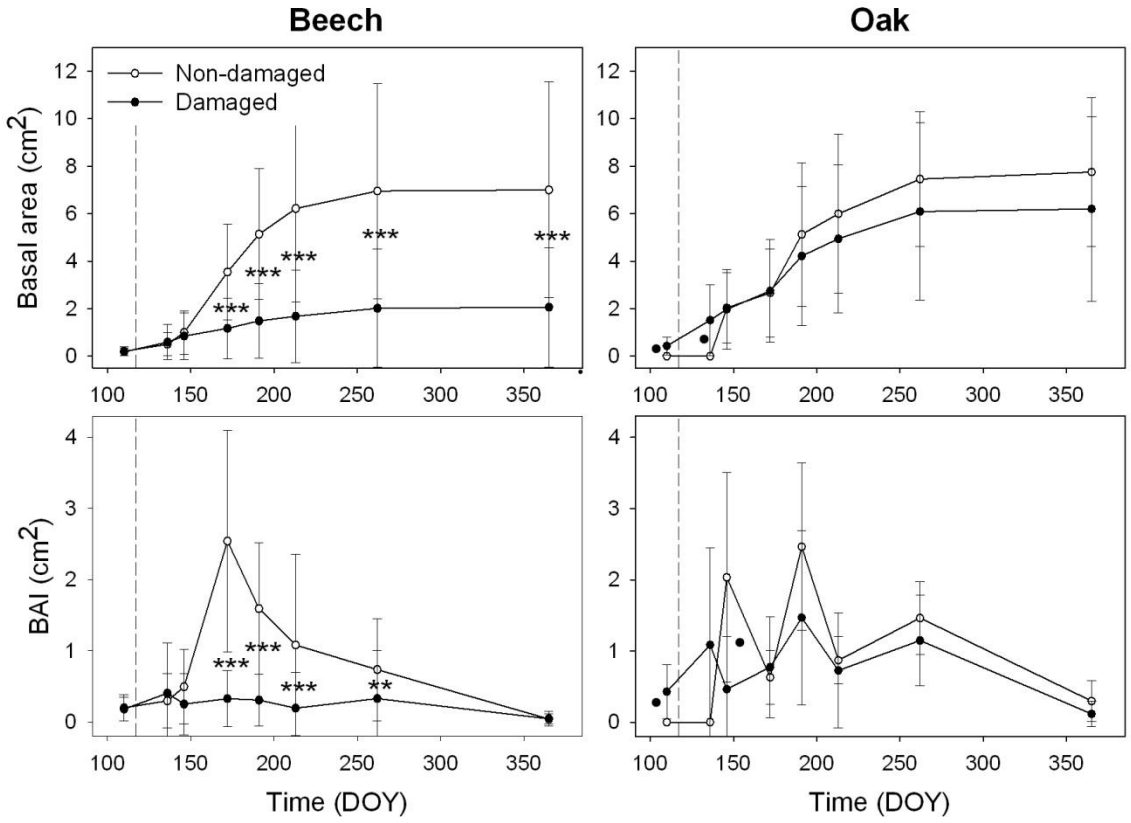

Figure 5.6. Stem radial-growth dynamics in beech and oak trees, either damaged or not damaged by a spring frost, throughout 2017. Data are means (± standard deviation bars). Significance levels: • $p < 0.1$, **$p < 0.01$ and ***$p < 0.001$, respectively. The spring frost is highlighted with dashed vertical lines. BAI is basal area increment and DOY is Julian day of the year.

Table 5.3. Means (and standard deviation) of growth-related phenological variables in beech and oak trees, either damaged or non-damaged by a spring frost, throughout 2017. *p*-values indicating the significance of differences between damaged and non-damaged trees are shown. The abbreviation "DOY" stands for Julian day of the year.

	Variable	Damaged	Non-damaged	*P*
Beech	DOY beginning	127 (16)	143 (10)	< 0.001
	DOY end	214 (36)	205 (17)	0.217
	DOY of maximum growth rate	168 (19)	173 (7)	0.171
	Growth length (days)	66 (49)	62 (24)	0.685
Oak	DOY beginning	115 (30)	138 (7)	0.182
	DOY end	231 (18)	231 (15)	0.505
	DOY of maximum growth rate	174 (16)	184 (13)	0.317
	Growth length (days)	116 (41)	93 (8)	0.182

5.3.4. Stand and forest level

The LAI in beech-dominated areas was significantly (p < 0.05) lower in 2017 than in 2015 (3.67 with 0.93 of standard deviation vs. 4.52 ± 0.96; i.e. LAI decreased 18.7% by an effect of the late frost). In areas dominated by oak, LAI decreased 15.4%, although the p-value of the difference was 0.09 (3.29 ± 0.94 in 2017 and 3.83 ± 0.93 in 2015).

Gaussian curves were the best fitting function for the NDVI time series. When analysing areas dominated by beech or oak species, the start of the 2017 spectro-phenological season occurred later for both (DOY 152 for beech and DOY 154 for oak) as compared to previous years (DOY 131 and 125, respectively) (**Fig. 5.7a** and **b**). On the contrary, the end of the spectro-phenological season occurred later in 2017 (26 days later in areas dominated by beech and 23 days later in areas dominated by oak). Hence, the length of the spectro-phenological season (time period between sprouting and senescence of leaves as defined from NDVI values) was 171 days for areas dominated by beech and 182 days for areas dominated by oak. The NDVI peak occurred later in both species in 2017 than in previous years (DOY 234 and 238 compared with DOY 211 and 213 for beech and oak, respectively). Highly significant differences (p < 0.001) were found in both beech- and oak-dominated stands between the NDVI 2014-2016 average series and the NDVI 2017 series.

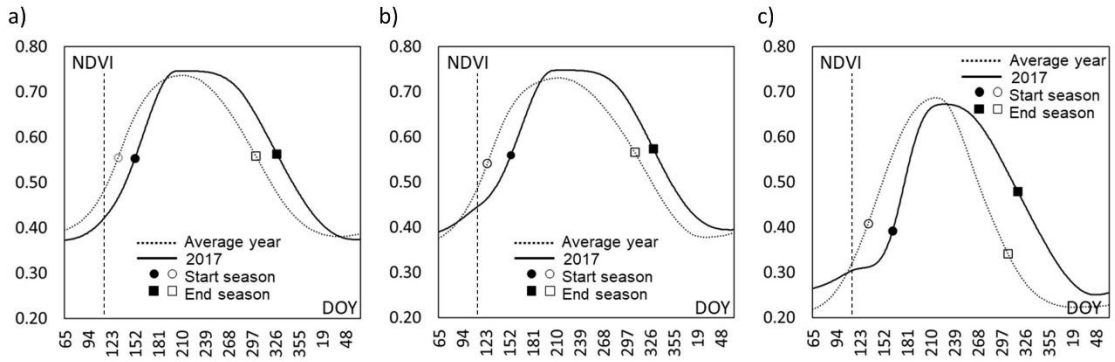

Figure 5.7. Gaussian model of the NDVI time series of "El Hayedo de Montejo" in areas dominated by beech (a) and oak (b) and in the entire forest (c). Start and end of spectro-phenological season were determined as the DOY at which the fitted curves reach 0.5 of their amplitude value, counted from the base level of the

left and right side of the curve, respectively. The spring frost is highlighted with dashed vertical lines. The abbreviation "DOY" stands for Julian day of the year.

Highly significant differences ($p < 0.001$) were found between the NDVI 2014-2016 average series and the NDVI 2017 series for the entire forest. The length of the spectro-phenological season in 2017 was 154 days at the forest level (**Fig. 5.7c**), that is, considering jointly the areas dominated by beech and oak, as well as by the most abundant *Q. pyrenaica* (see section 5.2.1. S*tudy site*). At this level the average length of the spectro-phenological season in the period 2014-2016 was 172 days. In 2017, the season started on June 12th (DOY 163), 30 days later than the start averaged over the three previous years. The 2017 NDVI peak value, an indicative of maximum photosynthetic activity, occurred on August 20th (DOY 232), 23 days later than on an average year (DOY 209), and was lower than in previous years. The end of the spectro-phenological season was later in 2017 than in previous years (DOY 317, compared to DOY 305 for the period 2014-2016). The spring frost impact on NDVI dynamics was similar for the whole forest, being negligible the effect of altitude (results not shown).

5.4. Discussion

5.4.1. Bud and leaf phenology: frost leaf scorching in early flushing trees delays senescence of new leaves

In beech, the sensitivity of bud bursting and leaf unfolding to temperature is mainly controlled by the photoperiod (Vitasse and Basler, 2013). This should make leaf phenology not particularly sensitive to warm winter conditions and prevent spring frost damage as compared with other deciduous tree species (Ma et al., 2019). Nevertheless, climate warming has advanced spring leaf unfolding of beech in Europe (Chen et al., 2018; Vitasse et al., 2018), particularly from the 1980s to 2000s; at different rates depending on site elevation (Kraus et al., 2016), local climate conditions or tree provenance (Chmura and Rozowski, 2002), reinforcing the controversy on the factors that govern leaf unfolding (Menzel et al., 2015; Zohner et al., 2016). In contrast,

oak depends largely on temperature for the right timing of leaf-out (Vitasse et al., 2014a). The study oak is one of the European deciduous species with latest leaf unfolding (Vitasse et al., 2014a), which allows this species minimizing the risk of frost damage. In the study area, bud opening and leaf unfolding occurs on average at approximately the same time in both species, although leaves usually expand and develop more slowly in oak than in beech (**Fig. 5.4a**). In 2017, leaf phenology was advanced in part of the trees (**Fig. 5.4b**) due to the warm winter (**Fig. 5.1b**) and the high temperatures that were reached during the week previous to bud opening, with daily minima above 10º C (**Fig. 5.1a**). Trees less sensitive to warming, which took longer to break dormancy, avoided frost damage to their leaves. The non-damaged oak trees sprouted five weeks after the frost-damaged trees, while the non-damaged beech trees sprouted three weeks later, possibly due to the greater importance of the photoperiod in beech trees.

The recovery of the crown in damaged trees differed between species. In an experimental study, Zohner et al. (2018) found that after a late frost event, oak leaves were developed more rapidly and reached their maximum development at the same time as the trees not subjected to the spring frost treatment, while beech trees damaged by frost had a slower leaf development compared to undamaged trees. Our results show that after the frost and subsequent sprout or re-sprout in non-damaged or damaged oak trees, respectively, leaf development (from bud opening to complete development) was completed faster than in an average year (**Fig. 5.4**). This rapid development partially compensated the delay in bud opening which affected oaks after the spring frost. On the contrary, in beech trees, the development of the different phenological phases was slower in 2017 than in an average year, something that is not observed in other studies (Awaya et al., 2009). In any case, NDVI data pointed out to a delay in leaf senescence in both species (**Fig. 5.7**), probably related to high autumn temperatures (**Fig. 5.1b**), which partially compensated for the reduction of the growing-season length caused by the spring frost. In addition to climatic factors, there may be other factors favoring delayed senescence. In this sense, recent studies suggest that autumn phenology is affected by the preceding spring development, with delays in leaf senescence compensating for late sprouts (Fu et al., 2014; Keenan and

Richardson, 2015; Liu et al., 2016; Signarbieux et al., 2017; Zohner et al., 2018). Other studies, however, do not show a delay in leaf senescence in frost-damaged trees (Awaya et al., 2009).

The fact that early-sprouting trees were damaged by frost, while late sprouting trees were not, hinders to unequivocally attribute differences between trees to an effect of the spring frost or the tree phenology. However, since previous studies have found no relationship between leaf phenology and some of the traits studied here, such as radial tree growth (Čufar et al., 2015), we believe that the differences observed between damaged and non-damaged trees can be mainly attributed to the spring frost effects.

5.4.2. Organ level: frost did not induce a carbon limitation to stem growth

Second-cohort leaves produced by damaged beech trees had lower LMA, SS, starch and NSC concentrations than leaves of the non-damaged beech trees (**Table 5.2**), in line with other studies of broadleaf species damaged by a late frost (St. Clair et al., 2009). Thinner leaves would have lower rates of photosynthesis because they would have less photosynthetic machinery (pigment-protein complexes and enzymes) per leaf unit area (Rodríguez-Calcerrada et al., 2008). Lower photosynthetic carbon uptake by leaves of the second cohort could explain their lower NSC concentrations. On the other hand, the second cohort of leaves of beech trees had lower C/N ratio and higher N concentration than the leaves of non-damaged beech trees. Higher mass-based photosynthetic capacity, which is highly linked to N concentration (Hoogesteger and Karlsson, 1992; Reich et al., 1999), would allow re-sprouted leaves to compensate, at least partially, for their lower LMA and photosynthetic machinery per leaf area. This result would be in accordance with previous studies on similar species where the second cohort of leaves produced after insect defoliation was more resource acquisitive (Fuenzalida et al., 2019). In contrast, no significant differences (**Table 5.2**) and lower relative differences (**Table 5.B1** in **Appendix B** of the Supplementary material) in leaf traits were found between leaves of the damaged and non-damaged

oaks, which would allow them to maintain similar rates of photosynthesis. In any case, our small sample size advocates for a cautious interpretation of these results.

The temporal dynamics of the concentrations of soluble sugars, starch and NSCs in stem sapwood for beech and oak throughout 2017 were very similar between damaged and non-damaged trees, and concurs with previous studies (Hoch et al., 2003). We found only significant differences of soluble sugars in two measurements in beech (**Fig. 5.5**). On June 1st, stem xylem soluble sugar concentrations were higher in damaged trees, possibly due to the mobilization of soluble sugars to form the second cohort of leaves (Klein et al., 2016). This is consistent with the drop in the soluble sugars concentration (see rate of change in **Fig. 5.5**), which occurred after the formation of the second cohort of leaves was completed by the damaged beech trees (**Fig. 5.4**). An alternative explanation to this result is the lower consumption of soluble sugars in stem growth in damaged trees, which was reduced by the late frost already by June 1st (**Fig. 5.6**) (Deslauriers et al., 2009). On the contrary, on September 28th, non-damaged beech trees had higher soluble sugar concentrations than damaged trees. The lower leaf (**Table 5.2**) and stem xylem soluble sugar concentrations on this date in the frost-damaged beech trees could be related to a lower resource acquisition capacity of the new leaves. Despite these punctual, small differences in NSCs between beech trees, NSC reserves were rather similar along the year in both species (being practically identical at the end of the year), indicating no limitation on carbon availability for growth (Hoch et al., 2003; Körner, 2003). The decrease in NSC concentrations in non-damaged beech trees observed after the end of the vegetative period (see rate of change in **Fig. 5.5**) could be related to the increased respiration rates in those trees showing more wood formation (Rodríguez-Calcerrada et al., 2019). Thus the higher resource acquisition capacity of non-damaged beeches would be partly compensated by increased respiration rates.

5.4.3. Tree level: frost reduced radial growth

Oak begins to produce early wood prior to or at the same time that budburst using NSC reserves whereas beech growth starts forming wood later, just after budburst,

and use mostly carbon assimilated by the leaves of the current year, with a maximal growth rate when the leaves are mature (Michelot et al., 2012; Puchałka et al., 2017). These different growth strategies could explain that NSC concentrations were more variable in oak than beech over time (**Fig. 5.5**), and the notable impact of frost on radial growth of beech (**Fig. 5.6**). The beginning of the radial growth in oak resulted in a drop in NSC concentrations, which was similar in damaged and non-damaged trees and showed a recovery during the growing season. The differences at $p < 0.1$ in radial growth between damaged and non-damaged oaks at the beginning of the growth period could be due to the earlier start of radial growth in damaged oaks, consistently with leaf phenology (**Fig. 5.4**), but this should be further checked using xylogenesis data. These differences, however, were later compensated when the growth of non-damaged oaks began. The clear reduction in radial growth in damaged beech trees suggest that carbon storage is an actively competing sink in beech trees and that, in case of defoliation, primary growth, crown recovery and carbon storage are favored over secondary carbon sinks as radial growth (Dietze et al., 2014; Miranda et al., 2020; Wiley et al., 2017).

Dendrometer data have lower precision as radial-growth measures than xylogenesis data derived from repeated microcore sampling. However, the results are similar when comparing both methods (Michelot et al., 2012). In addition, our results (**Table 5.3**) are consistent with those obtained in previous xylogenesis studies on beech (Martínez del Castillo et al., 2016). In all phenological variables related to radial growth, the variability in damaged beech trees was greater than in non-damaged trees (**Table 5.3**), probably due to differences in the vigor of the trees before the frost and/or the different impact of the frost among trees (showing between 50% and 100% of dead leaves on the trees classified as damaged). Accordingly, the most damaged beech trees and/or those with less vigor would reduce the length of their growing season while those that exhibited a moderate damage and/or were more vigorous would lengthen it. In fact, the largest BAI in damaged beech trees occurred between August 1st (DOY 213) and September 19th (DOY 262) while in non-damaged trees it occurred between May 26th (DOY 146) and June 21st (DOY 172) (**Fig. 5.6**).

5.4.4. Stand and forest level: frost reduces LAI and delays the NDVI annual peak

Our results showed a greater reduction of LAI in beech-dominated areas than in oak-dominated areas after the frost. This is in agreement with the reduction of total leaf area per twig, which was 29% in beech and 22% in oak (although only in beech the *p*-value of the difference was lower than 0.1) (**Table 5.2**). LAI reduction in our study was lower as compared to others (Awaya et al., 2009), possibly due to differences in the amount of damaged leaves and trees in the studied areas, and the existence of other non-damaged tree species in beech- and oak-dominated areas.

Fusing Landsat and MODIS satellite data provides synthetic data with high spatial and temporal resolutions that enable a detailed analysis of NDVI variations over time and precise determination of leaf emergence and senescence times. The NDVI peak value and the length of the 2017 spectro-phenological season were similar to previous years in areas dominated by beech and oak (**Figs. 5.7a** and **b**), suggesting that, although the vegetative period was delayed in 21 and 29 days, respectively, by incidence of the late frost, the total photosynthetic activity at stand level in 2017 was similar to previous years, partly due to the high autumn temperatures (**Fig. 5.1b**). As the study scale is enlarged, the detail is reduced. In this respect, it was possible to differentiate between frost-damaged and non-damaged trees at organ and tree levels, and to obtain the LAI *in situ* in areas where one or the other species dominate. However, when using satellite images there is a mixture of species at each of the areas considered, with intermingled damaged and non-damaged trees, which produces a blurring of the frost effects. For example, a LAI reduction in damaged trees could favor competing trees, and the overall NDVI at the stand level would not change.

The impact of the frost on the spectro-phenological season length was higher at the forest level (**Fig. 5.7c**) than in the areas dominated by beech or oak, with an 18-day reduction in 2017 compared to previous years. This is likely because the late-sprouting *Quercus pyrenaica*, with a much later phenology than beech and oak, is the most abundant species outside the areas dominated by beech and oak in the studied forest. Thus, the shorter 2017 growing season length would reflect the high contribution of *Quercus pyrenaica* to the overall forest NDVI trajectory. Although *Quercus pyrenaica*

was barely affected by the late frost (occurring two weeks before its average budburst time; in any case, during field surveys, it was the species that showed the least number of frost-damaged leaves), the drop of temperature at this time could have imposed a further delay in this species leaf emergence.

5.5. Conclusions

Early leaf-out in beech and oak trees caused by an unusually warm winter resulted in massive leaf scorching after a spring frost. Trees re-mobilized carbon and nutrient reserves to produce a second cohort of leaves. For beech, however, crown recovery was incomplete: leaves were smaller and thinner, and twigs had smaller leaf area than those of trees not affected by the frost. This did not have a significant impact on stem sapwood NSC concentrations, suggesting that beech trees prioritize maintaining carbon storage to secondary growth after leaf frost damage. Frost effects diluted as analyses scaled up from organ to forest levels, although some frost effects at stand level reflected the different organ- and tree-level sensitivity between species (e.g. the higher frost-induced reduction of LAI in beech stands). Delayed leaf senescence compensated for the frost-induced delay in carbon uptake, caused by leaf scorching and the time needed to form a second leaf cohort, alleviating the frost impact on the length of the vegetative period. Nonetheless, the differential response between the two study species may give oak a competitive advantage over beech, and may limit the current expansion of beech if the frequency of spring late frosts increases.

5.6. Acknowledgments

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Appendix A

To fuse the remotely sensed data, acquired daily by the Moderate Resolution Imaging Spectroradiometer (MODIS) sensor and at 8-16 days frequency by Landsat sensors (Operational Land Imager—OLI, and Enhanced Thematic Mapper Plus—ETM+), the Spatial and Temporal Adaptive Surface Reflectance Model (STARFM) algorithm was applied, obtaining synthetic daily surface reflectance data at medium spatial resolution (30 m) (Gao et al., 2015, 2006). Data from the MOD09GQ V6 collection acquired between 6 March 2014 and 12 January 2018 (to cover the 2014-2017 seasons) were downloaded from https://lpdaac.usgs.gov/. These surface reflectance data are acquired at 250 m spatial resolution at wavelengths 620-670 nm (band 1, red) and 841-876 nm (band 2, NIR) with a companion band of quality information. Fifty-eight Landsat images (path/row 201/031) free of clouds were available with variable frequency for the period of interest, and employed in the fusion process (**Fig. 5.3** of the document). MODIS images were projected to UTM 30N, registered to the Landsat data, and resampled to 30 m of spatial resolution. Synthetic daily data were then produced with STARFM, and masked with the MODIS quality band (resampled to 30 m). Daily series of the Normalized Difference Vegetation Index (NDVI) (eq. S1) were generated for the period 2014-2017.

$$NDVI = (NIR - red) / (NIR + red) \quad \text{(S1)}$$

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Appendix B

Table 5.B.1. Relative difference (see equation 1 in section 5.2.4. *Organ level*) between damaged and non-damaged trees of leaf and twig functional traits. LMA is leaf mass per area, SS is soluble sugars, NSC is non-structural carbohydrates, N is nitrogen and C is total carbon.

Variable	Beech	Oak
Individual leaf dry weight (g)	0,67	0,41
Individual leaf area (cm^2)	0,46	0,44
LMA ($g\ m^{-2}$)	0,19	0,01
Dry leaf weight per twig (g)	0,52	0,26
Total leaf area per twig (cm^2)	0,35	0,25
Number of leaves per twig	0,11	0,12
Sapwood section of the annual stems (mm)	0,14	0,05
Huber value	0,06	0,27
Average length of the apical buds (mm)	0,03	0,00
SS in leaves (%)	0,37	0,07
Starch in leaves (%)	0,32	0,10
NSC in leaves (%)	0,35	0,08
N in leaves (%)	0,42	0,06
C in leaves (%)	0,02	0,02
C/N ratio in leaves	0,44	0,09
Average	**0,30**	**0,15**

Appendix C

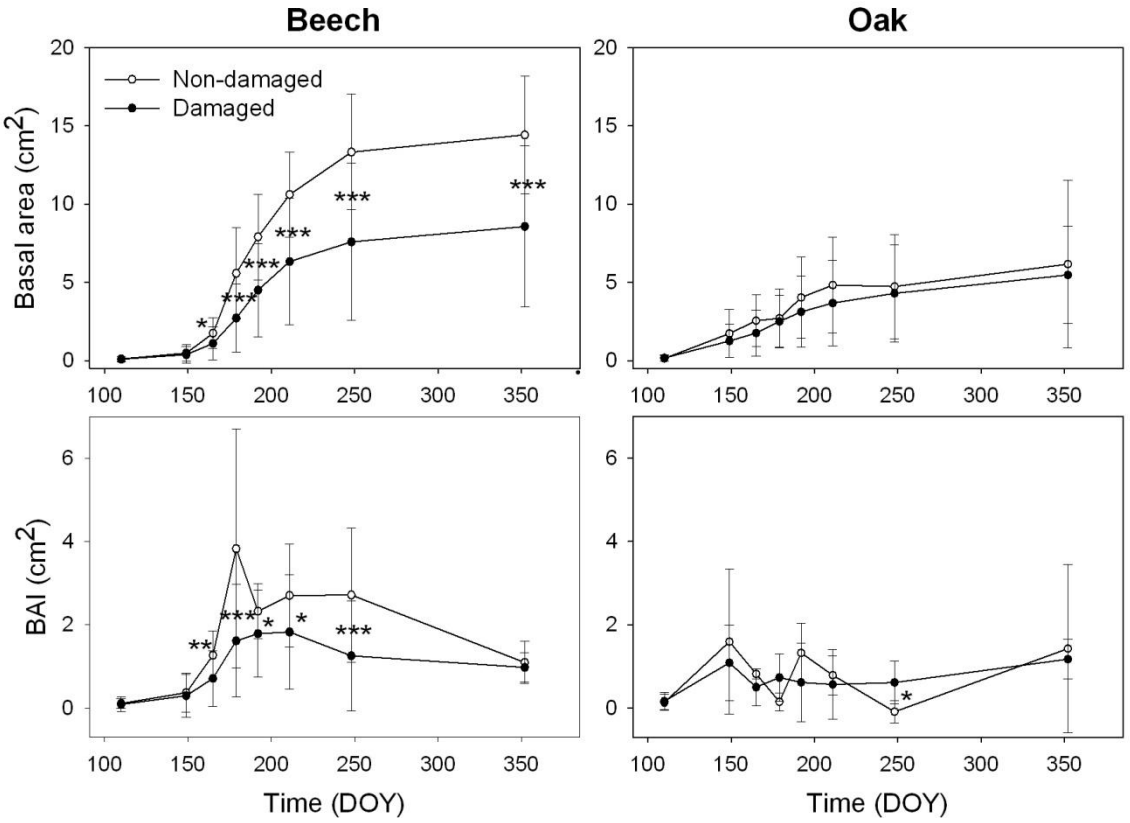

Figure 5.C.1. Stem growth dynamics in beech and oak trees, either damaged or not damaged by the 2017 spring frost, throughout 2018. Data are means (± standard deviation bars). Significance levels: * $p < 0.05$, ** $p < 0.01$ and *** $p < 0.001$, respectively. BAI is basal area increment and DOY is Julian day of the year.

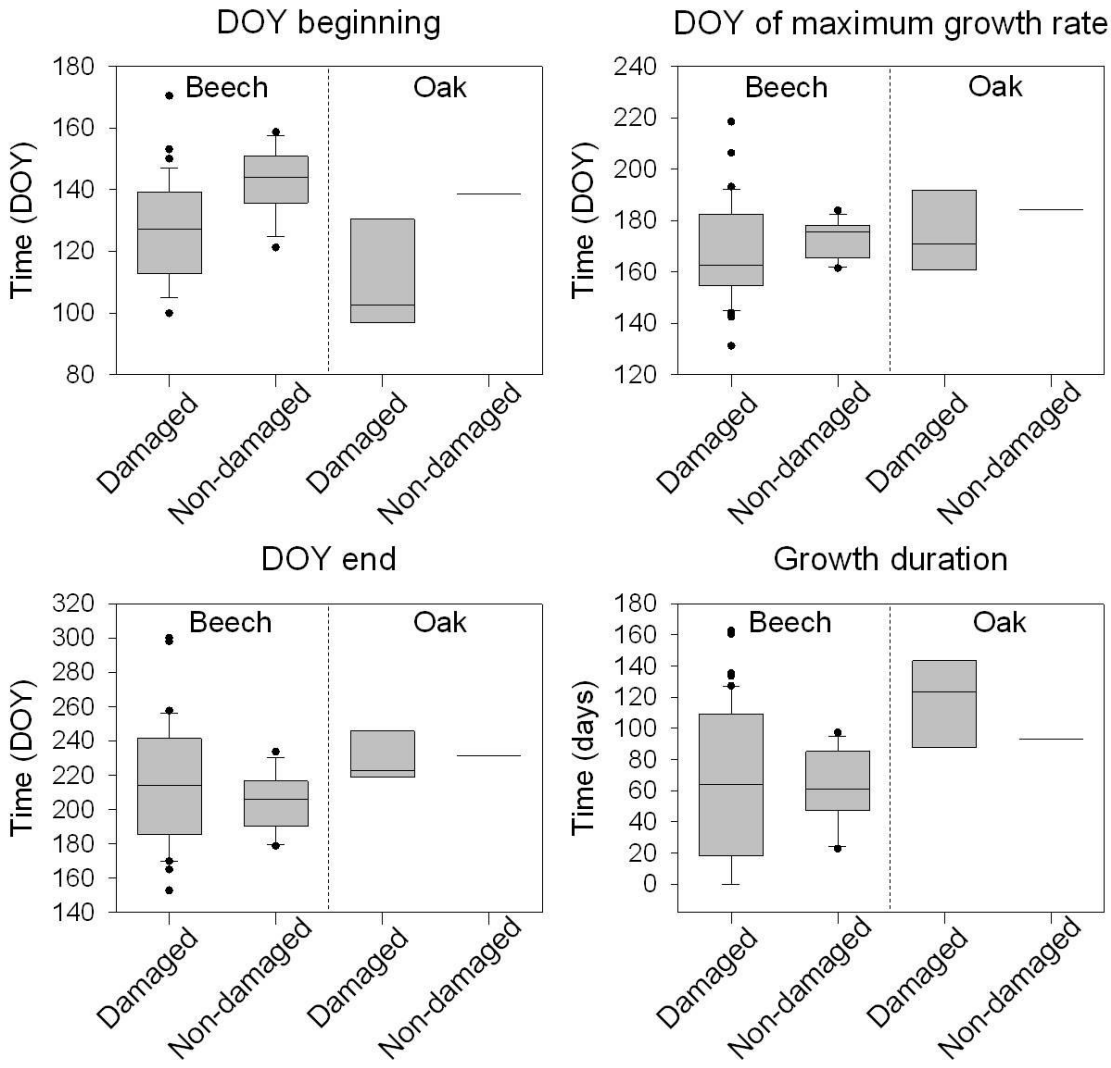

Figure 5.C.2. Box plots of growth-related phenological variables in beech and oak trees, either damaged or non-damaged by a spring frost, throughout 2017. The median, the 10th, 25th, 75th and 90th percentiles and the outliers are represented. The abbreviation "DOY" stands for Julian days of the year.

CAPÍTULO 6. IMPACT OF SUCCESSIVE SPRING FROSTS ON LEAF PHENOLOGY AND RADIAL GROWTH IN THREE DECIDUOUS TREE SPECIES WITH CONTRASTING CLIMATE REQUIREMENTS IN CENTRAL SPAIN

Este capítulo reproduce el texto del siguiente artículo ya publicado:

Rubio-Cuadrado, Á., Camarero, J.J., Rodríguez-Calcerrada, J., Perea, R., Gómez, C., Montes, F., Gil, L., 2021. Impact of successive spring frosts on leaf phenology and radial growth in three deciduous tree species with contrasting climate requirements in central Spain. Tree Physiol. tpab076. https://doi.org/10.1093/treephys/tpab076

Abstract

Rear-edge tree populations forming the equatorward limit of distribution of temperate species are assumed to be more adapted to climate variability than central (core) populations. However, climate is expected to become more variable and the frequency of climate extremes is forecasted to increase. Climatic extreme events such as heat waves, dry spells and spring frosts could become more frequent, and negatively impact and jeopardize rear-edge stands. To evaluate these ideas, we analyzed the growth response of trees to successive spring frosts in a mixed forest, where two temperate deciduous species, *Fagus sylvatica* (European beech) and *Quercus petraea* (sessile oak), both at their southernmost edge, coexist with the Mediterranean *Quercus pyrenaica* (Pyrenean oak). Growth reductions in spring-frost years ranked across species as *F. sylvatica* > *Q. petraea* > *Q. pyrenaica*. Leaf flushing occurred earlier in *F. sylvatica* and later in *Q. pyrenaica*, suggesting that leaf phenology was a strong determinant of spring frost damage and stem growth reduction. The frost impact depended on prior climate conditions, since warmer days prior to frost occurrence predisposed to frost damage. Autumn Normalized Difference Vegetation Index (NDVI) data showed delayed leaf senescence in spring-frost years and subsequent years as compared with pre-frost years. In the studied forest, the negative impact of spring frosts on *Q. petraea* and especially on *F. sylvatica* growth was considerably higher than the impacts due to drought. The succession of four spring frosts in the last two decades determined a trend of decreasing resistance of radial growth to frosts in *F. sylvatica*. The increased frequency of spring frosts might prevent the expansion and persistence of *F. sylvatica* in this rear-edge Mediterranean population.

6.1. Introduction

Climate change may increase the frequency and severity of extreme climate events, such as droughts and frosts, amplifying the consequences of climate change and challenging the ability of tree species to adapt to the new conditions (Stott 2016). In the case of spring frosts, i.e., below-zero temperatures occurring after the beginning of the vegetative period, Ma et al. (2019) and Zohner et al. (2020) have shown that the

frequency of their occurrence has changed differently across geographic areas and ecosystems, having generally increased since 1959 in Europe. These results reconcile apparently contradictory predictions of decreasing frost-risk in some studies (Scheifinger et al. 2003, Menzel et al. 2003, Dai et al. 2013, Morin and Chuine 2014, Hänninen 2016) and increasing risk in others (Cannell 1985, Kramer 1994, Inouye 2008, Gu et al. 2008, Augspurger 2013, Vitasse et al. 2014, Hänninen 2016, Abbas et al. 2017, Bigler and Bugmann 2018).

Spring frosts are critical events that could cause large damages to forest ecosystems, such as abrupt reductions in productivity, demographic changes, and shifts in species composition (Augspurger 2009, 2011), especially if these become commonplace due to climate change (Körner et al. 2016). At the tree level, a spring frost may damage the leaves, affecting their morphology, physiology and chemical composition (Klosson and Krause 1981a, 1981b, Sakai and Larcher 1987). The roots and live stem tissues are insulated by the soil and the outer bark, respectively, and are less likely to be damaged. Still, shallow fine roots, and young and large xylem conduits can be affected even by light frosts (Neuner et al. 2010, Ambroise et al. 2020). When the leaves are completely scorched by a spring frost, trees have to rebuild new foliage by mobilizing several-years-old reserves of non-structural carbohydrates and nutrients (D'Andrea et al. 2019). The time to rebuild a new leaf cohort depends in part on the capacity to remobilize the stored carbohydrates and nutrients, and, if the xylem was embolized by freeze-thaw cycles, it also depends on the capacity to produce new xylem conduits. The second cohort of leaves may be delayed by up to one month or more from the first cohort (Nolè et al. 2018, D'Andrea et al. 2019), resulting in a loss of photosynthesis. Once developed, this cohort of leaves may be less productive due to lower leaf nutrient concentrations, leaf size and/or total number of leaves (Awaya et al. 2009). Thus, frost-damaged trees experience a reduction in carbon uptake, which may lead to a reduction of up to 90% or more in radial growth (Dittmar et al. 2006). D'Andrea et al. (2021) showed that a spring frost can reduce the carbon stores of trees, especially starch concentrations, but they would return to a normal level during the following year. According to Körner (2015), in general, the rates of photosynthesis are controlled by the growth of tissues and, therefore, the repercussion of late frosts

on growth would mostly be due to the reduction of the vegetative period caused by the inability of cells to duplicate at low temperatures and by the hormonal signals induced. In any case, a single frost, but more likely a succession of frosts, could permanently damage the trees and kill them several years later, similar to the drought stress legacy effects that originate massive mortality episodes (Anderegg et al. 2015, Rodríguez-Calcerrada et al. 2017, Kannenberg et al. 2020).

In addition to the direct impact of the spring frosts damaging or killing the leaves, these events may have an indirect effect on trees by modifying the leaf phenology throughout the year of frost. In this sense, previous studies linked autumn phenology with the preceding spring development, so that delays in leaf flushing would be compensated for by delays in leaf senescence (Fu et al. 2014, Keenan and Richardson 2015, Liu et al. 2016, Signarbieux et al. 2017, Zohner et al. 2018). In contrast, the results obtained in other studies do not show such relationship (Awaya et al. 2009, Bascietto et al. 2018).

The leaf emergence in deciduous tree species is mainly coupled with minimum temperatures (Lenz et al. 2013, Körner et al. 2016, Vitasse et al. 2018), but other factors, such as photoperiod, may have a strong influence on the phenology of some species, such as *Fagus sylvatica* L. (Vitasse et al. 2009). Although deciduous trees exhibit similar safety margins to avoid leaf freezing damage by spring frost (i.e. similar difference between the minimum temperature experienced and the freezing resistance of the species; Lenz et al., 2013), the variability in frost resistance between species results in different leaf flushing times (Körner et al. 2016). Therefore, the leaves of early flushing species are more likely to be damaged by a spring frost than those of later flushing coexisting species (Augspurger 2009). The study of leaf phenology can be of great importance to know the direct impact of spring frosts and their indirect effects. Since phenological information based on direct observation is not frequently available, spectral indices like the Normalized Difference Vegetation Index (NDVI) are frequently used. The NDVI has shown effective to quantify changes in aboveground phenology after late frosts, and to estimate the canopy area affected and the loss in productivity, as well as the duration of the freezing stress effects (Bascietto et al. 2018, Greco et al. 2018, Nolè et al. 2018).

Rear-edge tree populations face harsh climate conditions and will be particularly affected by climate warming and the increase in extreme climate events (Hampe and Petit 2005). This is the case of some populations of temperate species in Mediterranean mountains (Rubio-Cuadrado et al. 2018a, Gazol et al. 2019), characterized by warm and dry summer conditions (Giorgi and Lionello 2008). In this work, we studied a mixed forest in central Spain, which is the southernmost distribution limit of *F. sylvatica* and *Quercus petraea* [Matt.] Liebl. (Pardo et al. 2004). Here, both temperate species are co-occurring with the Mediterranean *Quercus pyrenaica* Willd. These three broadleaved deciduous species show different leaf phenology, with *F. sylvatica* sprouting earlier than both *Quercus* species. Our targeted forest has been monitored since 1994. Since then, there have been conspicuous leaf damages due to spring frosts in at least one of the three dominant species in 1995, 2010, 2013 and 2017. Our objectives in this work were: (i) to evaluate the difference in growth among *F. sylvatica, Quercus petraea,* and *Quercus pyrenaica* during the years with spring frost, (ii) to study the post-frost growth resilience of the three tree species, and (iii) to analyze NDVI five-year series including a central episode of spring frost, relating them to frost-impact and post-frost effects. We hypothesized that: (i) the radial growth would be more affected in *F. sylvatica* than in the two *Quercus* species during the spring frost years due to the earlier leaf flushing of *F. sylvatica*; (ii) radial growth would recover more slowly in *F. sylvatica* than in both *Quercus* due to frost legacies; and (iii) stand primary productivity would be reduced during spring frost years and subsequent years, whereas leaf flushing and senescence would be delayed in spring frost years.

6.2. Materials and methods

6.2.1. Study area

The study site, “El Hayedo de Montejo”, is a mixed forest of 125 ha located at the “Sistema Central” mountain range, central Spain (41° 07’ N; 3° 30’ W), between 1,250-1,500 m a.s.l. The site aspect is east and the dominant species are the Mediterranean *Q. pyrenaica* and the temperate *F. sylvatica* and *Q. petraea*, with relative basal areas of

50%, 27% and 23% and mean diameters at breast height of 24.1, 16.5 and 19.9 cm, respectively. *F. sylvatica* and *Q. petraea,* as well as most individuals of *Q. pyrenaica*, originated from natural seedling in the studied forest, which contrasts with the coppice stands of *Q. pyrenaica* so characteristic in Central Spain (Valbuena-Carabaña et al. 2008). During centuries of firewood and cattle grazing, the forest had an open woodland structure of dispersed old and large trees, and scarce tree recruitment (Pardo and Gil 2005). However, in 1961 cattle grazing was forbidden, and the last logging took place in 1962 (López Santalla et al. 2003, Gil et al. 2009). These changes in land use have favored an increase in the number of trees during the last decades.

The climate is continental Mediterranean, with 900 mm of mean annual rainfall and a prolonged dry period during July and August. The mean annual temperature is 9.5 ºC. Temperatures below 0º C occur from November to February, but spring frosts are also common. The soil has been classified as humic cambisol and the horizon A reaches 50 cm of depth on average, enabling considerable water storage during dry periods (Pardo et al., 1997).

6.2.2. Frost events

Climate data were obtained from a meteorological station set up in the study forest in 1994, at 1,406 m a.s.l., and managed by the Natural Systems and Forest History research group of "Universidad Politécnica de Madrid", Spain. Missing data of the minimum temperatures were estimated by a linear regression model of data from this station and those from "Pantano El Vado" local station (41° 0' 13'' N and 3° 18' 7'' W, 910 m a.s.l.; AEMET, Spanish Meteorological Agency), located ca. 21 km away from the forest:

$$Tmin_{\text{El Hayedo de Montejo}} = 0.864\ Tmin_{\text{Pantano El Vado}} + 0.1547 \quad (R^2 = 0.76) \qquad (1)$$

Since 1994, there have been four spring frosts damaging the leaves of one or more of the tree species coexisting in the studied forest (**Fig. 6.1**). The spring frosts occurred in April 23-26th 1995, when temperatures reached a negative peak of -2.4 ºC;

May 3-6th 2010, when temperatures reached -2.0 °C; April 27-28th 2013, when temperatures reached -3.8 °C; and April 27-28th 2017, when temperatures reached -4.6 °C. Furthermore, in these four years there were also secondary frosts occurring after the main damaging frost, which might have increased the impact produced. Secondary frosts occurred in: May 12-13th 1995, when temperatures reached -1.25 °C; May 14th 2010, when temperatures reached -1.85 °C; May 17-18th 2013, when temperatures reached -0.16 °C; and May 1st 2017, when temperatures reached -1.63 °C.

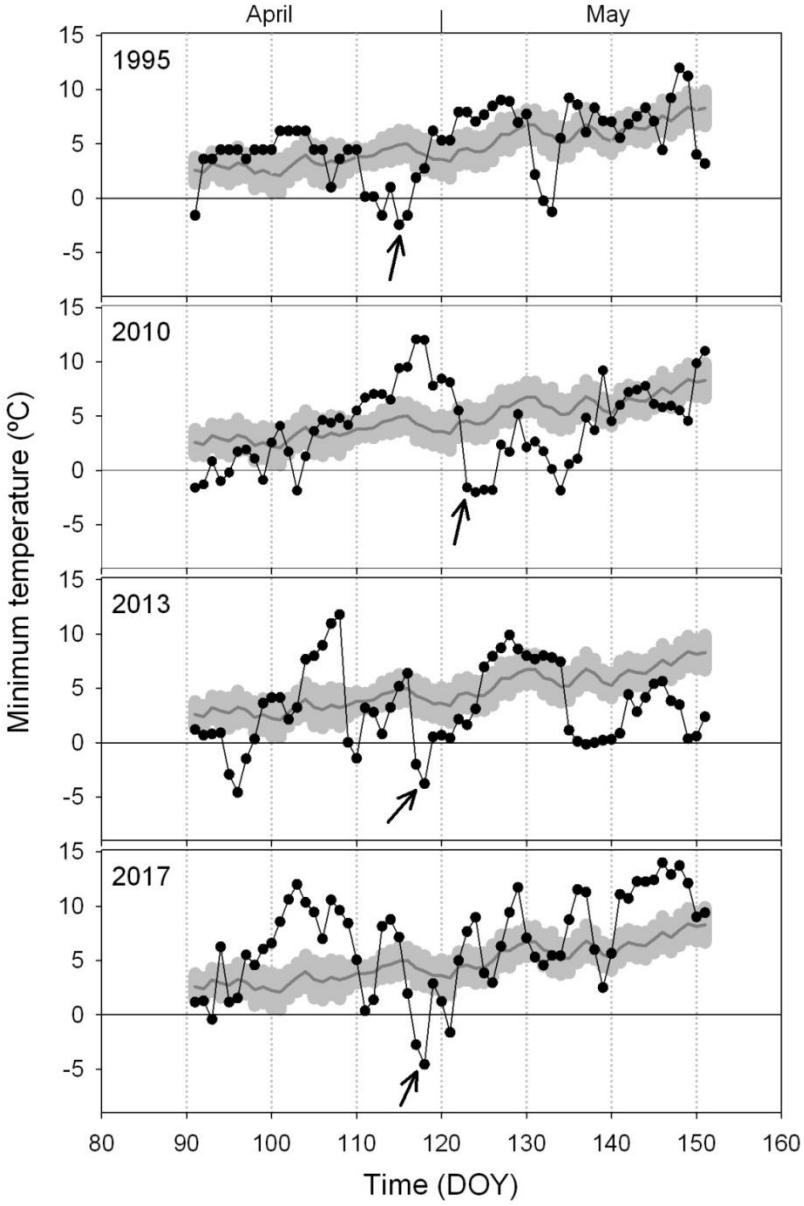

Figure 6.1. Daily minimum air temperatures from April to May in years with frost damage (1995, 2010, 2013 and 2017) compared with an average year for the 1994-2018 period (with dark grey lines for the mean and light grey area for the 95% confidence intervals). The arrows point to days in which the frost damage was observed. DOY stands for Julian day of the year.

6.2.3. Leaf phenology

In order to relate the time of bud opening and leaf emergence with the spring frost damage, we retrieved a phenological inventory performed in ten *F. sylvatica* adult trees, eight *Q. petraea* and eight *Q. pyrenaica* adult trees (Millerón et al. 2012). In this inventory three twigs from branches oriented to the south and three twigs from branches oriented to the north were monitored on each tree once a week during the whole vegetative period to examine leaf phenology from 2006 to 2011. Sampled twigs were located in the lower part of the live crown (< 3 m height). One-year-old twigs were selected, unless they had less than five buds, in which case longer (older) twigs were selected. For each twig, the number of still-dormant buds and the foliar phenophase were annotated following Millerón et al. (2012). We recorded leaf flushing time (in Julian day of the year; DOY) and then we estimated its temporal range for each species, with the median and the 10^{th}, 25^{th}, 75^{th} and 90^{th} percentiles, since neither the buds of a given tree nor the individuals of a given species sprouted simultaneously.

6.2.4. Sampling and dendrochronological analyses

Between 20 and 24 dominant or codominant trees distributed throughout the forest were selected for each species. In each tree two wood cores were extracted at 1.3 m (always perpendicular to the maximum slope), using a Pressler increment borer, and the diameter at breast height (DBH) of each tree was measured at 1.3 m with a caliper during autumn of 2018. Cores were mounted on wooden supports and carefully sanded until tree rings were clearly visible. After a visual cross-dating, tree-ring widths were measured to the nearest 0.01 mm using the semi-automatic LINTAB measuring device with the TSAP-Win software (RINNTECH, Heidelberg, Germany). Then, visual cross-dating was further verified with the COFECHA program (Holmes, 1997). Growth data are available in Rubio-Cuadrado et al. (2020b). Altitudes for sampled trees were retrieved from a Digital Terrain Model of 25 m spatial resolution (PNOA, Instituto Geográfico Nacional, Spain).

We calculated the mean tree-ring width series for each individual tree. These series were subsequently transformed into basal area increments (BAI), as this variable is better than tree-ring width for capturing growth trends and accounting for the increase in size and age of stems (Biondi and Qeadan, 2008). The BAI was calculated as follows:

$$BAI = \pi(r_t^2 - r_{t-1}^2) \quad (2)$$

where r_t and r_{t-1} are the stem radii at the end and the beginning of a given annual ring.

When cores did not contain the pith, the missing core length was estimated to calculate the BAI by subtracting the core length to the tree radius measured in the field without bark. Bark thickness was estimated based on tree diameter using equations fitted to the data from the Second Spanish National Forest Inventory (DGCONA, 1998). Functions used to estimate the bark thickness of *F. sylvatica* (C_{Fs}), *Q. petraea* (C_{Qpe}) and *Q. pyrenaica* (C_{Qpy}) are the following:

$$C_{Fs} = -0.00001\ DBH^2 + 0.0284\ DBH + 0.3545 \quad (3)$$

$$C_{Qpe} = 1.4407\ DBH^{0.4071} \quad (4)$$

$$C_{Qpy} = 7.4422 \ln(DBH) - 23.845 \quad (5)$$

The final species chronologies were built by averaging annual BAIs across all trees of the same species. The statistical quality of each chronology or mean site series was checked via Expressed Population Signal (EPS) (Speer, 2012), which measures replication and coherence as compared to a perfectly replicated chronology. A threshold value of EPS > 0.85 was considered reliable to represent the mean BAI series of each tree species. The description of dendrochronological variables of cored trees is shown in **Table 6.S1** of the Supplementary material.

6.2.5. Impact of spring frosts on tree growth

Individual tree growth reduction due to spring frost events was characterized via the tree-ring series, calculating resistance (*Rt*) and resilience (*Rs*) indices (Lloret et al., 2011) as:

$$Rt = BAI_i / BAI_{i-6} \quad (6)$$

$$Rs = BAI_{i+1} / BAI_{i-6} \quad (7)$$

where BAI_i is the BAI observed in the frost year, BAI_{i-6} is the mean BAI calculated over the 6 years preceding the frost year, and BAI_{i+1} is the observed BAI in the year that follows the frost year. *Rt* and *Rs* were calculated using the *pointRes* package in R (van der Maaten-Theunissen et al., 2015). Although these indices are typically calculated over periods of 3-4 years after the stress event when studying drought effects (Gazol et al., 2017; Rubio-Cuadrado et al., 2018a), we considered just one year after the spring frosts because it is apparently the only year in which growth is affected, in addition to the year of the spring frost itself (see Results), and because we only have growth data up to 2018 to study the effect of the 2017 frost. With regard to the time period before the spring frost, we chose six years to buffer the effect of the other spring frosts on these indices. In this respect, the 2010 spring frost is affecting the BAI_{i-6} of the 2013 spring-frost year, which in turn affects the BAI_{i-6} of the 2017 spring-frost year. We applied the Kruskal–Wallis test by ranks for independent samples and the Conover's post-hoc test, with the Bonferroni method to adjust *p*-values, to compare the *Rt* and *Rs* means between *F. sylvatica*, *Q. petraea* and *Q. pyrenaica*.

An additional analysis of the growth reductions produced by spring frost was the Superposed Epoch Analysis (SEA) (Lough and Fritts, 1987). SEA identifies the link between discrete events and continuous time processes and tests the probability of such association occurring by chance. We used the double-bootstrap SEA methodology described by Rao et al. (2019) to evaluate growth departures from mean values for the years with spring frost and the 2-year of pre- and post-disturbance periods. To calculate the SEA we used ring-width indices as input variable. To obtain these indices we removed biological trends of the raw tree-ring widths by calculating the detrended

chronologies for each species using the ARSTAN program (Holmes, 1997). We applied a double detrending procedure to remove long-term growth trends (Holmes et al., 1986). First, we fitted a negative exponential curve to raw ring-width data, to remove the effect of age and of low competition during the first years of the growth series, that is, during the establishment of the analyzed trees in the open woodland (before cattle grazing ban). Second, we fitted a 32-year long cubic smoothing spline, to remove the low-frequency stand dynamics signals. The autocorrelation of the resulting detrended time series was removed by applying a first-order autoregressive model but reintroducing into the residual series part of the low-frequency signal in order to retain climatically-related autocorrelation in growth.

6.2.6. Spring frost effect on spectral phenology

The impact of frosts on spectral phenology was studied with an NDVI dataset recently developed by Vicente-Serrano et al. (2020) over the entire peninsular Spain and Balearic Islands for the period 1981-2015. This dataset is based on the National Oceanic and Atmospheric Administration–Advanced Very High Resolution Radiometer (NOAA–AVHRR) afternoon images, and has a 15-day temporal resolution, with 1.1 km^2 spatial resolution. In order to compare the annual spectral dynamics of pre-frost and post-frost periods with the frost year dynamics, we averaged the NDVI annual series of three groups of years: 1993-1994, 2008-2009, and 2011-2012, representing the two-year pre-frost period; 1996-1997, 2011-2012, and 2014-2015, representing the two-year post-frost period; and 1995, 2010 and 2013, representing the frost year. The 2017 frost period was not included in this analysis as there were not enough data available. TIMESAT software (Eklundh and Jönsson, 2017) was used to determine the spectro-phenological start, length, and end of the season, as well as the peak NDVI values and DOY of occurrence. The start- and end-of-season parameters were determined based on seasonal amplitude, defined as the difference between the base and maximum NDVI values for each season. The start occurs when the left part of the fitted curve reaches a percentage of that amplitude value, counted from the base level, and the end of season is defined similarly but for the right side of the curve. These values were

calibrated with data from the phenological inventory. The corresponding parameters for pre-frost, frost, and post-frost years were analyzed and compared. Gaussian curves were adjusted to the pre-, post-, and frost series to enable comparison. Finally we tested the differences in NDVI values for each date (averaged for each group of years) between pre-frost, frost, and post-frost years with Mann-Whitney *U* tests.

6.3. Results

6.3.1. Leaf emergence

Excluding the outliers (values below or above the 10^{th} and 90^{th} percentiles, respectively), leaf flushing started in *F. sylvatica* and *Q. petraea* almost simultaneously, in DOYs 113 and 110, respectively, while *Q. pyrenaica* leaf flushing started later, in DOY 123 (**Fig. 6.2**). Keeping the outliers out of the analysis, the variability in leaf flushing time was higher in *Q. petraea*, and to a lesser extent in *Q. pyrenaica*, than in *F. sylvatica*. That is, the leaf emergence period was longer in *Q. petraea* (35 days) and *Q. pyrenaica* (31 days) than in *F. sylvatica* (17 days). This means that the four late frosts recorded in the forest since 1994 affected a higher proportion of developing shoots in *F. sylvatica* than in *Q. petraea*, while *Q. pyrenaica* was hardly affected by these events. In this respect, the spring frost of 2010, which coincided with the period of leaf phenology monitoring (2006-2011), occurred when approximately 50, 25 and 0% of the buds were opening in *F. sylvatica*, *Q. petraea* and *Q. pyrenaica*, respectively (**Fig. 6.S.1** in Supplementary material).

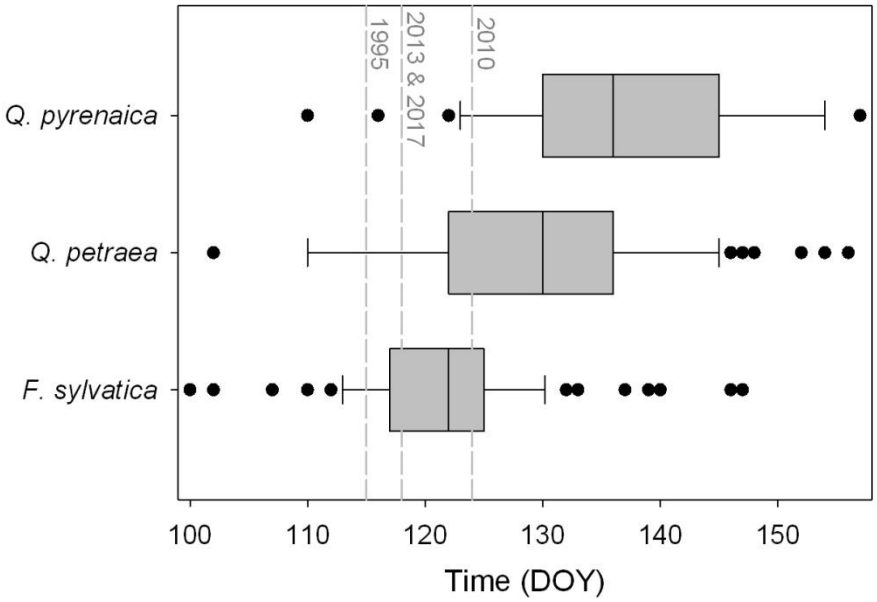

Figure 6.2. Box-plots for leaf emergence time (Day of year; DOY) in *F. sylvatica*, *Q. petraea* and *Q. pyrenaica* monitored during the period 2006 to 2011. The spring frosts are marked with dashed vertical lines. The median, the 10th, 25th, 75th and 90th percentiles and the outliers are represented. Due to the numerous outliers the graphs are truncated on the right.

6.3.2. Spring frost effects on basal area increments

F. sylvatica trees exhibited the highest variability in growth. The coefficients of variation for the growth series since 1980 were 0.280, 0.169 and 0.174 for *F. sylvatica*, *Q. petraea* and *Q pyrenaica*, respectively. *F. sylvatica* was also the species with the greatest growth reductions in the years with spring frost, namely 1995, 2010, 2013 and 2017 (**Fig. 6.3**). These growth reductions were similar to the reduction in growth registered in 2016, the year with the warmest and driest summer since 1994 (see average annual climate data in **Fig. 6.S.2** of the Supplementary material).

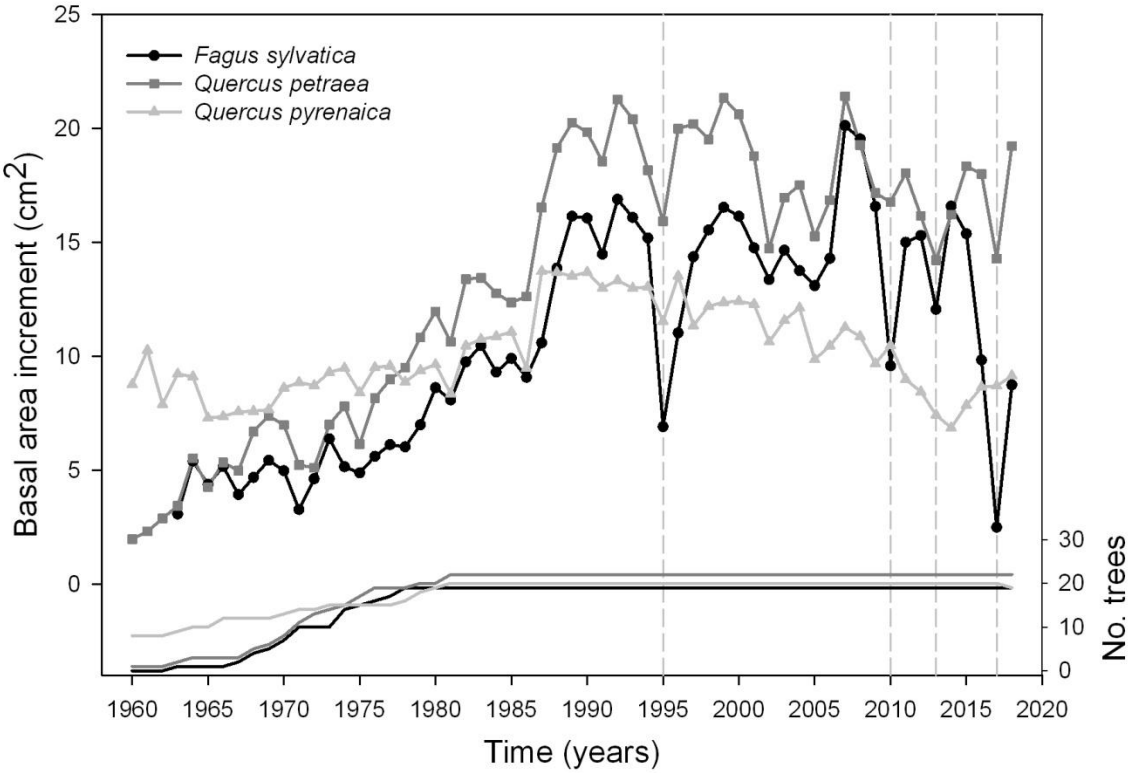

Figure 6.3. Basal area increment and number of cored trees with growth rings (right y-axis) dating back to 1960. The spring frosts are marked with dashed vertical lines. The forest is monitored since 1994, therefore possible earlier frosts are missing.

Q. petraea also exhibited a reduction in growth during the years with spring frosts, but of lower magnitude than that of *F. sylvatica*. In the spring frost year of 2010, the growth of *Q. petraea* was similar to that of the previous year (**Fig. 6.3**). In addition, *Q. petraea* presented similar growth reductions during 2002, one of the coldest years of the series, and 2005, the driest year of the series (**Fig. 6.S.2**). In contrast, *Q. pyrenaica* showed little year-to-year growth variability during the entire series, and no remarkable growth reductions during frost years. This species showed a decreasing trend in growth since 1987, when it reached the maximum growth.

F. sylvatica had significantly lower growth frost-resistance (*Rt*) than both *Quercus* species in the years 1995, 2010 and 2017 (**Fig. 6.4**). In 2013, no significant differences in resistance were found among species. Differences in resistance between *Q. petraea* and *Q. pyrenaica* were not significant on any year except for 2017. While this result suggests that both species had a similar behavior during the frost years, the

complementary Superposed Epoch Analysis (SEA) shows that only *F. sylvatica* and *Q. petraea* (not *Q. pyrenaica*) exhibited significant relationship between frost events and growth reductions (**Fig. 6.5**).

Growth frost-resilience (*Rs*) was significantly lower in *F. sylvatica* than in both *Quercus* after the 1995 and 2017 frosts (**Fig. 6.4**), although no significant relationship was found between these values and frost events according to the SEA (**Fig. 6.5**). In any case these low growth values during the years 1996 and 2018 observed in *F. sylvatica* did not seem to correspond to the climatic conditions of those years, which were cool and rainy (and potentially favorable for growth) during all or a large part of the year (see monthly temperature and precipitation of the frost and subsequent years in **Fig. 6.S.3** of the Supplementary material). *Q. pyrenaica* had significantly lower *Rs* than the other two species after the 2010 and 2013 frosts (**Fig. 6.4**); however, this result seemed to be more related to the decreasing growth trend of this species (**Fig. 6.3**) than to the spring frosts (**Fig. 6.5**).

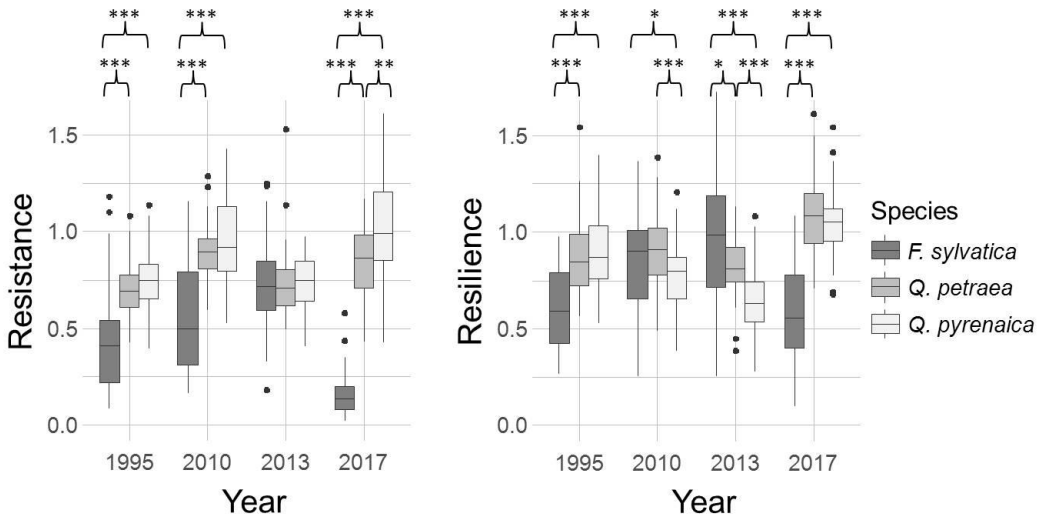

Figure 6.4. Resistance (*Rt*) and resilience (*Rs*) indices for *F. sylvatica* (dark-grey box-plots), *Quercus petraea* (medium grey box-plots) and *Quercus pyrenaica* (light-grey box-plots) for the four years with spring frost recorded since 1994. Significance levels of the differences: * $p < 0.05$, ** $p < 0.01$ and *** $p < 0.001$, respectively.

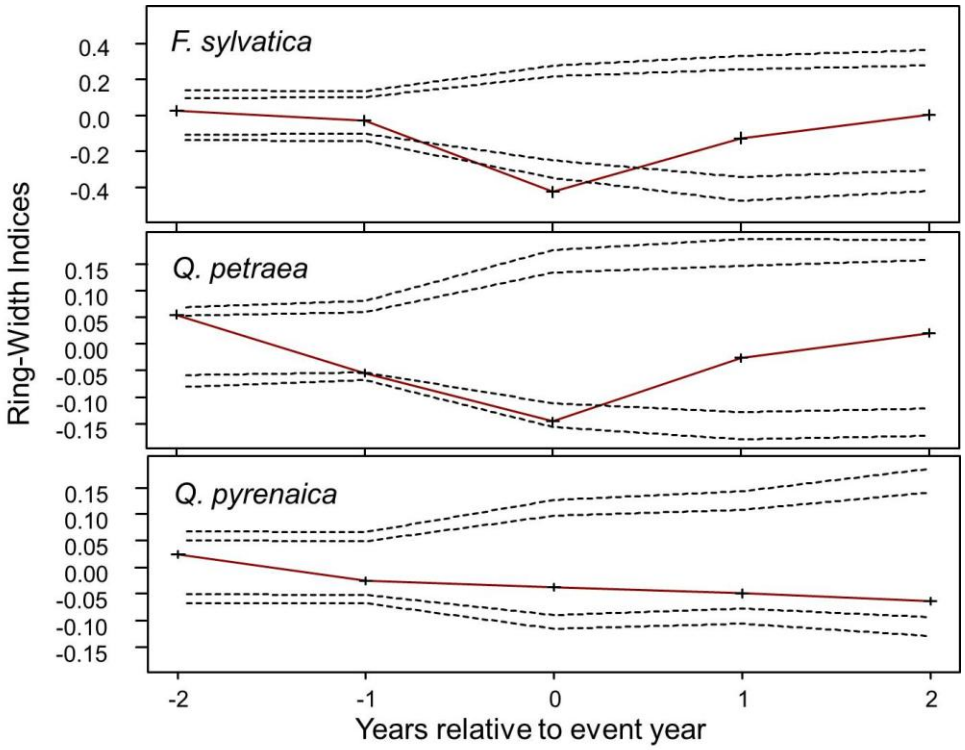

Figure 6.5. Superposed epoch analyses showing positive and negative growth departures from mean growth values for the year with frost damage (year 0) and 2 years before (years -1 and -2) and after this event (years +1 and +2). Values were calculated considering the four years with frost damage (1995, 2010, 2013 and 2017). The dashed lines denote the thresholds of significance ($P < 0.05$ and $P < 0.01$).

The resistance index (*Rt*) has been calculated for the entire growth series since 1977 (**Fig. 6.6**) to analyze whether there were other factors, apart from spring frosts, inducing growth drops. The most important growth drops in *F. sylvatica* occurred in years with spring frosts (2017, 1995 and 2010, ordered from lowest to highest resistance), while in both *Quercus*, since growth declines during these years were not so severe, the lowest resistance occurred in years other than those with spring frost (2002 for *Q. petraea* and 2014 for *Q pyrenaica*). The three tree species showed a decreasing trend in *Rt* between 1977 and 2018. The slopes of the time-resistance regressions were -0.008, -0.002 and -0.003 for *F. sylvatica*, *Q. petraea* and *Q pyrenaica*, respectively, being significant for *F. sylvatica* ($P = 0.007$) and *Q. pyrenaica* ($P = 0.027$), but not for *Q. petraea* ($P = 0.201$).

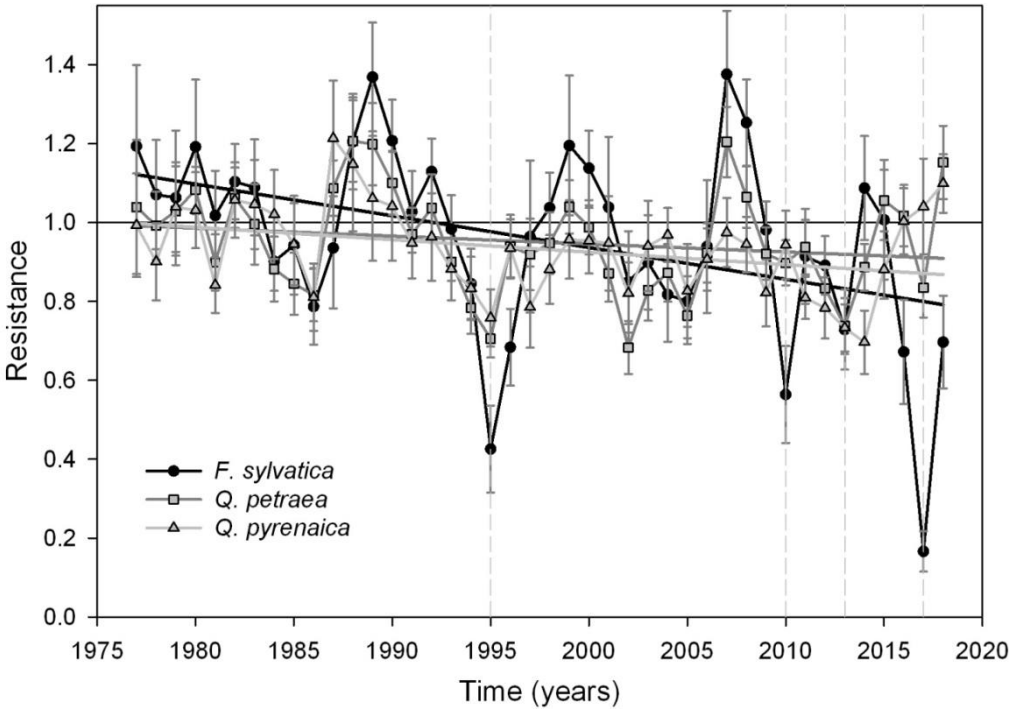

Figure 6.6. Trends in resistance index (*Rt*; i.e. the BAI in a given year divided by the mean BAI over the 6 previous years) since 1977. Data are means and 95% confidence intervals per species. Linear regressions were fitted to each species. The spring frosts are marked with dashed vertical lines.

6.3.3. Spring frost effect on spectral phenology

There were no significant differences in the maximum NDVI values between the years in which the spring frost occurred and the pre- and post-frost years. The length of the spectro-phenological season (time period between sprouting and senescence of leaves as determined from NDVI values) was 168 days for pre- and post-frost years and 196 days for frost years (**Fig. 6.7**). In pre-frost years the start and end of the spectro-phenological season occurred in DOY 113 and 281, respectively; in frost years occurred in DOY 127 and 323, respectively; and in post-frost years occurred in DOY 127 and 295, respectively. Thus, both the beginning and end of the spectro-phenological season occurred earlier in pre-frost years than in frost years, with intermediate behavior in the post-frost years. Similar performance occurred with the timing of NDVI peak, with a DOY of 169, 190 and 183, for the pre-frost, frost and post-frost years, respectively. In any case, none of these differences were statistically significant.

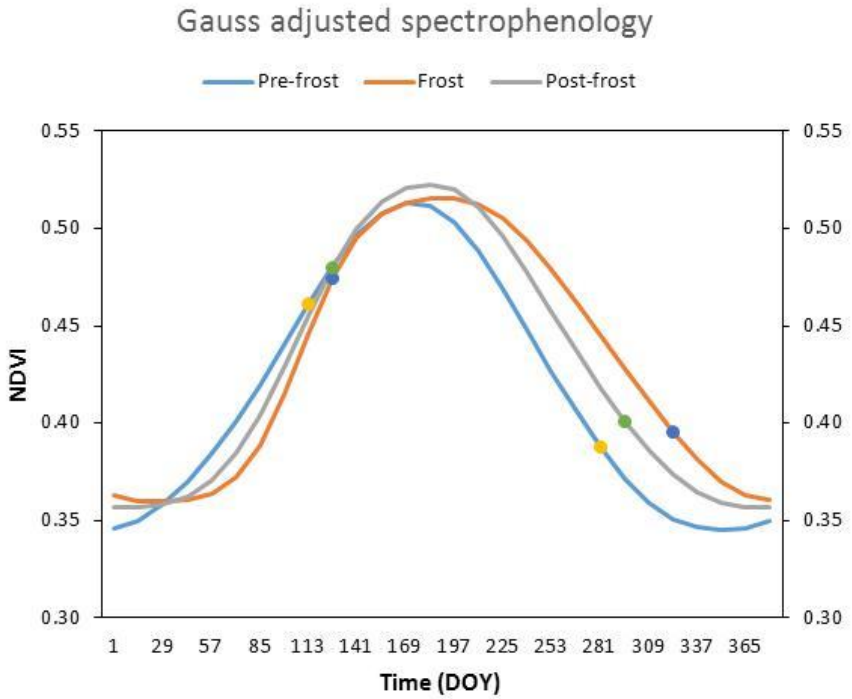

Figure 6.7. Gaussian model of the intra-annual NDVI time series in the years with frost damage (1995, 2010 and 2013; 2017 was not included due to lack of data), in the two years prior to frost years, and in the two years after frost years. Start and end of spectro-phenological season were pointed with dots.

6.4. Discussion

6.4.1. Large stem growth reductions caused by spring frosts in F. sylvatica, not in Q. pyrenaica

Spring frosts caused high growth reductions in *F. sylvatica*, moderate growth reductions in *Q. petraea* and no significant growth reductions in *Q. pyrenaica* (**Figs. 6.3** and **5**). Based on visual observations of leaf malformation and scorching after spring frosts, and the negative relationship between frost-induced growth reduction and leaf flushing time across species, we suggest that leaf phenological stage (and associated probability of frost leaf damage) is a major determinant of reduced growth during frost years, and sometimes the year afterwards. This hypothesis is reinforced by the results obtained in Allevato et al. (2019), where damage severity in beech trees was related with the phenological stage.

According to previous studies, the freezing temperature of the leaves of *F. sylvatica* and *Q. petraea* is around -5 ºC (Lenz et al., 2013); to our knowledge no work has studied the freezing temperature of *Q. pyrenaica* leaves. However, there are other factors influencing leaf damage by frost, such as air relative humidity, wind, prior temperature conditions, rate of temperature drop and, especially, the duration of the frost (Min et al., 2020). Indeed, the four spring frosts recorded in the study forest reached temperatures between -2.0 and -4.6 ºC, and were preceded by weekly warm periods (**Fig. 6.1**).

Meteorological conditions preceding spring frosts may condition frost impact on the leaves and on stem growth. In *F. sylvatica*, the largest growth declines occurred in 1995 and 2017 (**Fig. 6.4**), which had warmer winters and springs than normal (**Fig. 6.S.3a**), being 2017 the warmest year in the series (**Fig. 6.S.2**). Warmer late-winter temperatures would induce an earlier leaf emergence (Vitasse et al., 2009) and, conversely, in cold years such as 2010 (**Fig. 6.S.3a**), leaf emergence would be delayed (compare **Fig. 6.2** with **Fig. 6.S.1**). Therefore, for a same frost date (all spring frosts studied in this work occurred on a very similar date, April 28 ± 5 days), the impact is greater in warm years with advanced phenology, that is, with a higher proportion of buds sprouted and therefore susceptible to be affected by frost. The relationship between high temperatures leading to advanced phenology and frost damage, which has also been shown by Sangüesa-Barreda et al. (2021), can lead to confounding the effects of spring frosts with those of droughts, and to erroneous conclusions on the factors that control growth when the spring frost events are unknown and not analyzed. This may be the case for the growth drops of 1995 and 2017, when drought effect would be secondary since drier years with similarly high temperatures, such as 2015 (**Fig. 6.S.2**), did not produce a growth decrease in *F. sylvatica*. Despite leaf phenology of *Q. petraea* being more temperature-dependent than that of *F. sylvatica* (Vitasse et al., 2009), the impact of spring frosts on growth was greater in *F. sylvatica* (**Fig. 6.4**), making this species more vulnerable to these extreme climate events (**Fig. 6.5**). The lower impact of spring frosts on *Q. petraea* growth is partly explained by the lower damage suffered by the leaves, which would be in turn related to its later leaf phenology (**Fig. 6.2**), but it is also explained by the differences between tree species

when faced with the same damage. In this sense, the loss of a cohort of leaves caused by a spring frost seems to produce a decrease in growth in *F. sylvatica* but not in *Q. petraea* (Rubio-Cuadrado et al. 2021). The lower *Q. petraea* growth produced in frost years (**Fig. 6.5**) seems to be due mostly to a delay in phenology, possibly caused by the freeze-thaw events (Tedla et al., 2020), rather than to a direct effect of the damage suffered by the frozen leaves. Effectively, according to a previous study conducted in the same area (Rubio-Cuadrado et al., 2021), the *F. sylvatica* trees damaged by the 2017 frost due to their earlier leaf flushing lost the first cohort of leaves, suffered a great delay in the emergence of the second leaf cohort and, consequently, reduced their growth drastically compared to those undamaged, with later leaf flushing. However, undamaged and damaged *Q. petraea* trees showed similar radial growth increments. Although the damaged *Q. petraea* trees also lost the first cohort of leaves, both undamaged and damaged trees suffered a similar delay in the emergence of the first and second leaf cohorts, respectively. The differences between tree species in the response to the same damage may be related to the fact that wood formation in *F. sylvatica* generally begins after budburst and use mostly carbon assimilated by the leaves of the current year, with a maximal growth rate when the leaves are mature (Čufar et al. 2008, Michelot et al. 2012), whereas in ring-porous species such as *Q. petraea*, wood formation begins before budburst using carbon reserves (Michelot et al. 2012, Puchałka et al. 2017, Gričar et al. 2017). Regarding *Q. pyrenaica*, it did not suffer any significant drop in growth compared to the years without spring frost (**Fig. 6.5**) due to its much more delayed phenology (**Figs. 6.2** and **6.S.1** in Supplementary material).

Ice formation in the xylem can occur at the relatively high subfreezing temperatures registered in the four spring-frost years (-2 to -4.6 ºC), particularly in young and large xylem conduits (Davis et al., 1999; Neuner et al., 2010). Hence, a priori, the larger xylem vessels of *Q. petraea* and *Q. pyrenaica* would make the xylem of these species more sensitive to freezing than that of *F. sylvatica* (Cavender-Bares, 2005; Davis et al., 1999). However, our results suggest that differences in leaf phenology between species (earlier in *F. sylvatica*) are more important drivers of the extent of growth reductions caused by spring frosts than differences in xylem vessel

diameter and theoretical xylem vulnerability to freeze-thaw embolism (lower in *F. sylvatica*).

Drought effects on growth were less noticeable than those of spring frosts, especially in *F. sylvatica*. Being "El Hayedo de Montejo" one of the southernmost European forests where *F. sylvatica* and *Q. petraea* coexist, and knowing that these species, specially *F. sylvatica*, are drought sensitive (Scharnweber et al., 2011), we expected to find important growth reductions due to droughts (Hampe and Petit, 2005; Hanewinkel et al., 2013), as it has been found in other nearby similar forests (Rubio-Cuadrado et al., 2018a) and also in northern populations subjected to a more humid climate (Scharnweber et al., 2011; Vannoppen et al., 2020). However, the main growth reductions in *F. sylvatica* were due to spring frosts (**Figs. 6.3** and **6.6**), being 2016 the only year in which the growth decline in *F. sylvatica* seemed to be related to drought (**Fig. 6.S.2** in Supplementary material). Although rainfall was very low during summer months for the 1994-2018 period (31 mm on average), leaf predawn water potential, a surrogate of soil water availability to plants, is rarely below -0.5 MPa in *F. sylvatica* and -1 MPa in *Q. petraea* and *Q. pyrenaica* adult trees during summer in the study area (Cano et al., 2013; Rodríguez-Calcerrada et al., 2019). This is possibly due to high soil water retention and tree rooting depth in the study site. In any case, previous studies have shown a reduced impact of summer drought on the growth of southern beech forests, probably resulting from a shortening of the radial growth period, so that most of the growth is concentrated in the wettest period (spring and early summer), thus reducing the possible impact of summer droughts (D'Andrea et al. 2020, 2021). These results would confirm that trees in rear-edge populations can display a high resistance to drought (Cavin and Jump, 2017), although they could be particularly vulnerable to other climate extremes, such as spring frosts, particularly under continental conditions (Sánchez de Dios et al., 2020). In *Q. petraea*, only in 2005 the reduction in growth coincided with a severe summer drought; the rest of growth reductions coincided with spring frosts or, in 2002, with a possible reduction in the vegetative period related to low temperatures (**Fig. 6.S.2**). *Q. pyrenaica* showed very low sensitivity to both dry years and spring frosts years, which suggests a better adaption to the Mediterranean mountain climate. The negative growth trend since

1987 observed in this species is due to the increase in competition occurred in the study forest in recent decades, which would favor the more competitive *F. sylvatica* (Rubio-Cuadrado et al., 2020a).

6.4.2. Frost legacies: decreasing resistance index and delayed senescence

The growth resilience after the spring frosts of 1995 and 2017 was significantly lower in *F. sylvatica* than in both *Quercus* species (**Fig. 6.4**). Although there was no statistically significant relationship between the spring frosts and the *F. sylvatica* growth declines of 1996 and 2018 based on the SEA (**Fig. 6.5**), these declines are difficult to explain only by the climate of these years, with cool temperatures and higher winter and spring rainfall than average (see resistance index in **Fig. 6.6**, and climate in **Figs. 6.S.3c, d**). A legacy of spring frosts on growth was observed in a previous work performed in the same forest (Dorado-Liñán et al., 2017). In this work, centennial *F. sylvatica* trees exhibited a growth reduction after the 1995 frost that had not yet reversed in 2013. Compared to our results, obtained in 50-years-old *F. sylvatica* trees (**Table 6.S1** in Supplementary material), the reduction in growth for almost a decade in larger, centennial *F. sylvatica* trees suggests a different frost legacy on growth depending on tree size or age, which should be further investigated. In any case, this age effect does not seem to be generalizable (Jiao et al., 2020), and there may be other factors that condition it, such as the effect of past land use or the vigor decline after a certain age.

Since the resistance index (*Rt*) is a relative and dimensionless index, it is not expected to find any trend in its dynamics. This index has not changed over the last decades in *Q. petraea*, but it has decreased in *Q. pyrenaica* and *F. sylvatica* (**Fig. 6.6**). For *Q. pyrenaica* this result is probably due to its negative growth trend (**Figs. 6.3** and **6.6**) associated to increasing competition (Rubio-Cuadrado et al., 2020a). However, for *F. sylvatica*, there was no significant effect of competition on growth (Rubio-Cuadrado et al., 2020a). Therefore, the reduced *Rt* in recent decades is likely a legacy of spring frosts. The legacies of extreme climate events on growth have been attributed mainly to physiological factors, specially to damages in the hydraulic system and limitations in

the availability of non-structural carbohydrate reserves (Adams et al., 2017; Hacke et al., 2001; Peltier and Ogle, 2019; Schönbeck et al., 2018; Timofeeva et al., 2017). In line with this, the availability of non-structural carbohydrates is probably not a reason of lower resilience (*Rs*) of *F. sylvatica*. Previous studies showed a reduced impact of late frosts on non-structural carbohydrate concentrations of *F. sylvatica* (Rubio-Cuadrado et al. 2021); and when a significant impact occurs this is rapidly reversed (D'Andrea et al. 2019, 2021). In addition, the lower proportion of parenchyma and non-structural carbohydrate concentrations in the sapwood of *F. sylvatica* as compared with that of the two *Quercus* species may be compensated by a higher sapwood depth (Rodríguez-Calcerrada et al. 2015). In any case, the decreasing trend of *F. sylvatica* growth may be explained by several causes. First, the increase in spring frost frequency itself and its cumulative effects on *Rt*; that is, the accumulation of late frosts at the end of the period considered (1994-2018), which influences the slope of the regression line between time and *Rt*. Second, the greater impact of the 2017 spring frost resulted from both the lower temperatures reached during the frost days (**Fig. 6.1**) and the fact that it was the warmest year in the series (**Figs. 6.S.2** and **6.S.3**), which would increase the number of sprouted buds when the frost occurred. Third, the occurrence of spring frosts on overlapping recovery times, which can potentially affect ecophysiological memory, amplifying a negative carbon balance or damaging the xylem and reducing hydraulic conductivity (Szejner et al., 2020). And fourth, the increase in temperatures and the decrease in precipitation that have occurred in the last decade (**Fig. 6.S.2**) may have magnified the negative effect of spring frosts due to increasing drought stress.

The spatial resolution of the NDVI dataset employed (1.1 km^2) prevents from obtaining detailed information to distinguish the frost effects on different species, but other factors affecting species phenology and frost impact, such as the aspect or altitude (Allevato et al. 2019) are fairly homogeneous in the study area (see section 2.1 *Study area*). The information obtained should be understood as representative of the overall response of the forest, where the NDVI increases gradually as the different species sprout: early sprouting species should determine the start of the steep rise of NDVI whereas the late sprouting determines the end. The NDVI dataset shows another legacy of the spring frost, a delay in autumn leaf senescence in the frost year and also

but less markedly in the following year (**Fig. 6.7**). This trend is consistent with a previous study conducted in the same forest about the consequences of the 2017 frost on stem, shoot and leaf functional traits, including leaf phenology using shorter NDVI time series, but with higher temporal and spatial resolution (Rubio-Cuadrado et al., 2021). Here, we found no significant differences in NDVI between years, but this is partly because of the low number of spring-frost years with NDVI data (1995, 2010 and 2013) and the low spatial resolution of the dataset analyzed. Large-scale studies performed in the Northern Hemisphere have shown a significant positive relationship between the timing of leaf flushing and leaf senescence in approximately 20% of the studied areas (Liu et al., 2016). Temperate, mixed beech-oak forests would be one of the forest types in which this relationship would be particularly strong (Fu et al., 2014). To our knowledge, there are no studies reporting frost legacy effects on stem growth or leaf phenology. However, such effects are possible, given the relationship between leaf life span, growth and carbon gain, and frost effects on all three variables during the frost year (Rubio-Cuadrado et al., 2021). More detailed research is needed on this subject.

6.4.3. Management implications

In forests where *F. sylvatica* coexists with oaks, beech trees tends to outcompete the other species (Rohner et al. 2012, Petritan et al. 2017, Rubio-Cuadrado et al. 2018b) due to its greater competitiveness and shade tolerance (Hein and Dhôte 2006, Manso et al. 2015). Likewise, in the studied forest, *Q. pyrenaica* is the most abundant species of the upper stratum (measured in basal area), but *F. sylvatica* dominates in the proportion of seedlings and saplings (Vélez Olalde 2016). However, *F. sylvatica* was more sensitive to spring frosts and, according to Sangüesa-Barreda et al. (2021), the frequency and geographic extent of spring frost events affecting this species has increased rapidly in the last two decades in southern Europe. If this trend continues, *F. sylvatica* may see their development compromised by more recurrent climatic extreme events. Therefore, the foreseeable retraction of oaks in benefit of *F. sylvatica* may bring about a loss of ecosystem resilience. Management strategies aimed at

maintaining a mixed stand with diverse light-regeneration niches to favor the presence of *F. sylvatica* and both oaks species in the understory should be considered as a means to promote forest resilience. In addition, promoting the regeneration of *F. sylvatica* phenotypes showing late leaf emergence could improve the resilience of this species to spring frosts.

6.5. Conclusions

In a mixed beech-oak rear-edge population, *F. sylvatica* showed a decades-long trend of decreasing resistance of growth and higher growth sensitivity to spring frosts than two co-occurring oak species (*Q. pyrenaica* and *Q. petraea*), suffering severe radial growth reductions, often stretched over two years, after the occurrence of the spring frosts. Leaf flushing time (earlier in *F. sylvatica*) and leaf damage (more frequent and severe in *F. sylvatica*) appeared to be more determinant factors of stem growth reduction during the spring-frost year than stem xylem anatomy, based on the consideration that narrower vessels of *F. sylvatica* are, a priori, less vulnerable to freeze-thaw embolism. Spring frosts caused significant growth reductions in *Q. petraea* trees too, although of lower magnitude and only during the year of the spring frost. By contrast, the spring frosts did not affect *Q. pyrenaica* growth. Although the studied forest is located at the southernmost distribution limit of *F. sylvatica* and *Q. petraea*, the impact of spring frosts on their growth has been considerably greater, especially in *F. sylvatica*, than the drought impacts. Taking into account the expected increase in the frequency of these events in Europe, spring frosts may become one of the greatest hazards for these rear-edge *F. sylvatica* populations.

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6.7. References

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Supplementary material

Table 6.S.1. Description of dendrochronological variables of cored trees. Statistics were calculated for the maximum length for each species. Standard errors are shown in parentheses.

	F. sylvatica	***Q. petraea***	***Q. pyrenaica***
Mean DBH (cm)	28.6 (1.0)	32.8 (1.3)	33.6 (2.5)
Mean / maximum length of series (years)	47 (1) / 129	45 (1) / 59	64 (7) / 143
Mean tree-ring width (mm)	2.43 (0.04)	2.74 (0.04)	1.77 (0.03)
Mean basal area increment (cm^2)	10.6 (0.3)	13.4 (0.3)	10.5 (0.2)
Mean basal area increment since 1971 (cm^2)	11.7 (0.3)	15.4 (0.3)	10.6 (0.2)
Mean correlation between trees	0.33	0.29	0.17
Expressed Population Signal since 1971	0.94	0.94	0.88

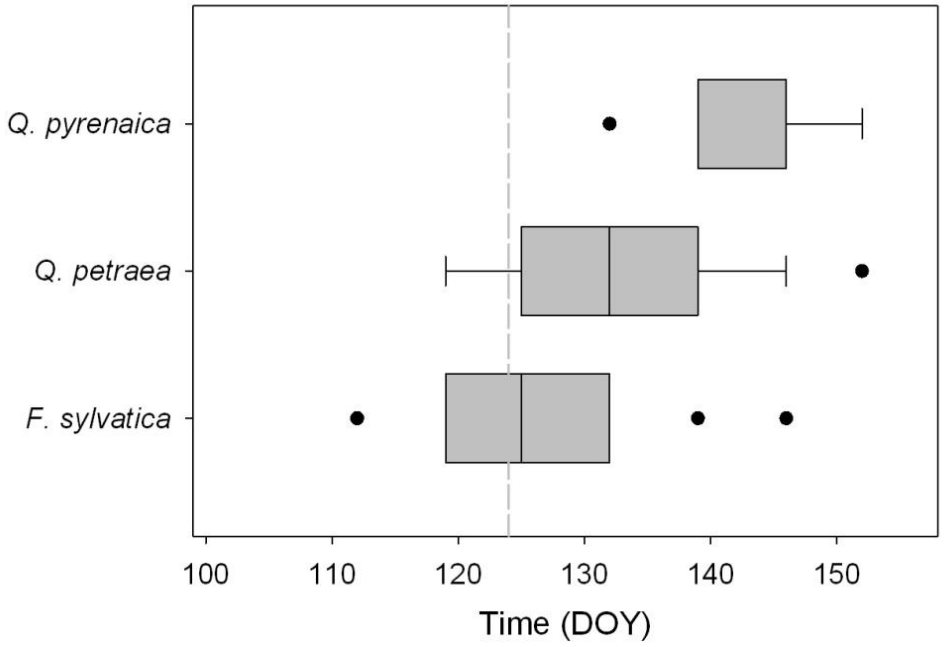

Figure 6.S.1. Chronogram of average leaf emergence time in *F. sylvatica*, *Q. petraea* and *Q. pyrenaica* for the year 2010. The spring frost is highlighted with a dashed vertical line. DOY stands for Julian day of the year. The median, the 10^{th}, 25^{th}, 75^{th} and 90^{th} percentiles and the outliers are represented.

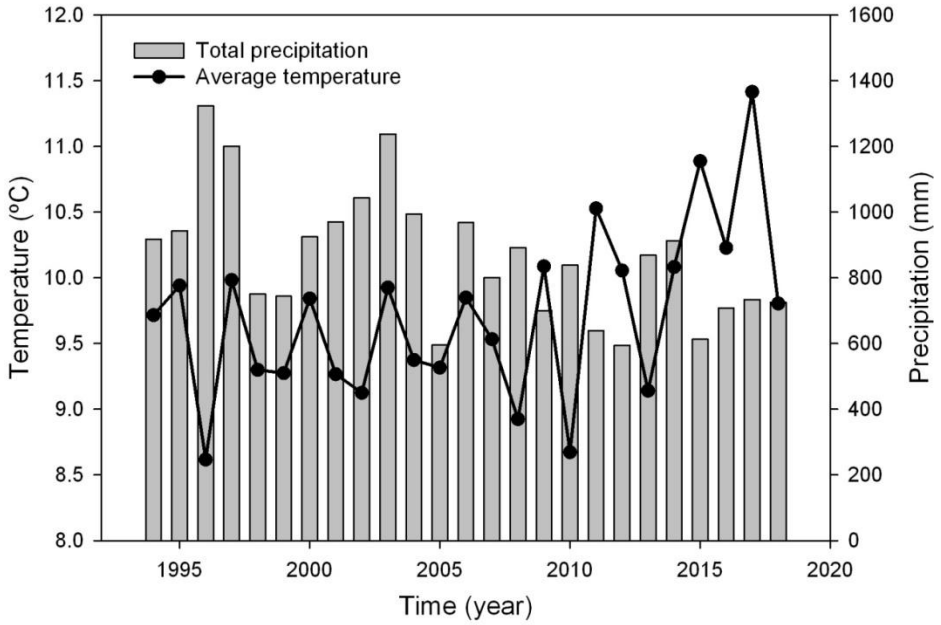

Figure 6.S.2. Average annual temperatures (line) and precipitations (bars) for the 1994-2018 period in the study period.

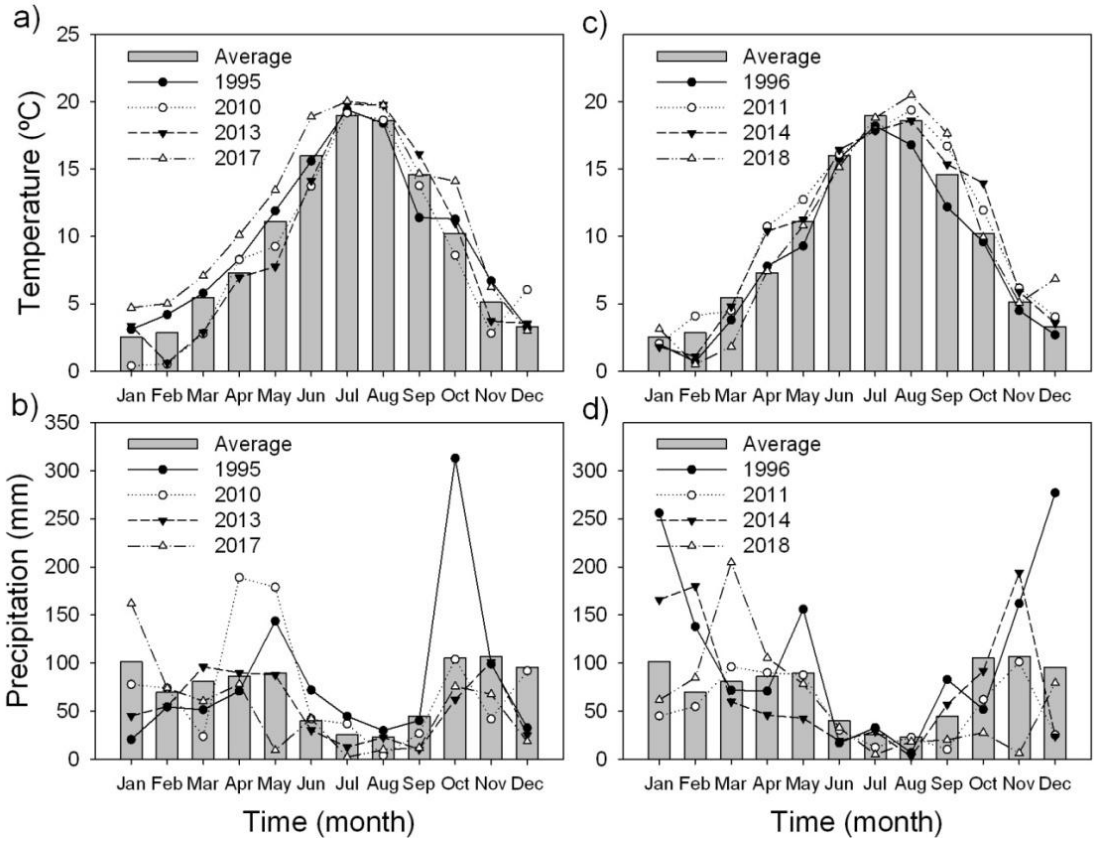

Figure 6.S.3. Average monthly temperatures (a y c) and total precipitations (b y d) in the years with frost damage (a y b) and in the subsequent years (c y d) compared with an average year (considering the 1994-2018 period).

CAPÍTULO 7. DISCUSIÓN GENERAL

En total se han realizado 5 estudios sobre 4 especies arbóreas distribuidas en 2 espacios naturales. Las especies que se mezclan o cohabitan cambian de un espacio natural a otro, estando presente el haya y el roble albar en Picos de Europa y El Hayedo de Montejo, el rebollo en El Hayedo de Montejo y el abedul en Picos de Europa. En este capítulo se han integrado los resultados obtenidos para cada una de las especies en los distintos trabajos realizados y los dos espacios naturales estudiados. En el caso del abedul, al ser una especie que solo ha sido objetivo en el capítulo 2, en este apartado de discusión general no se puede aportar nada nuevo a lo ya comentado en la discusión de dicho capítulo, por lo que a él remitimos.

7.1. Evolución general del clima

En general no se ha detectado una tendencia en las precipitaciones a lo largo del siglo XX, manteniéndose, en los dos sitios estudiados, unos valores anuales medios constantes a lo largo de todo el periodo (**Figs. 2.1** y **4.2**). Aunque en Picos de Europa se ha detectado una tendencia decreciente significativa, ésta solo se da en la serie de clima estimado CRU, pero no en la serie de datos reales de la AEMET (**Fig. 2.1**). Por el contrario, la temperatura sí que ha mostrado una tendencia creciente a lo largo del siglo XX, especialmente a partir de la década particularmente fría de 1970.

7.2. Haya

7.2.1. Relaciones entre el crecimiento y el clima

En los hayedos estudiados, situados en Picos de Europa y en la Sierra del Rincón (El Hayedo de Montejo), dada su localización marginal dentro de la distribución de la especie (**Fig. 2.A.1**, en los apéndices del capítulo 2) y su sensibilidad a la sequía (Scharnweber et al., 2011), esperábamos encontrar una fuerte relación entre el crecimiento y el clima, producto de una fuerte sensibilidad climática de la especie por

vivir en unas condiciones limitantes. Sin embargo, en ninguno de los estudios se han encontrado relaciones fuertes entre el clima y el crecimiento (**Figs. 2.3**, **4.4** y **4.5**). De hecho, en el hayedo de Montejo de la Sierra, siendo uno de los hayedos más meridionales de Europa, el crecimiento del haya mostró menores correlaciones con el clima que el roble albar o el rebollo (**Figs. 4.4** y **4.5** y **Tabla 4.2**). Igualmente, en Picos de Europa la temperatura mostró una relación directa con el crecimiento (**Fig. 3.3** y **3.4**), tal y como ocurre en hayedos más septentrionales (Lévesque et al., 2016; Toïgo et al., 2015), produciéndose un efecto negativo sobre el crecimiento únicamente cuando las altas temperaturas coinciden con bajas precipitaciones. Esta falta de correlación entre el crecimiento del haya y el clima posiblemente está relacionada con el relieve montañoso y la altitud (900-1600 m en Picos de Europa y 1250-1500 m en El Hayedo de Montejo) a la que se encuentran estas masas, donde las condiciones de crecimiento se asemejan a las de otros hayedos situados en áreas húmedas y frescas (Lebourgeois et al., 2005). En este sentido, también se encontró un posible efecto fertilizador del CO_2 (**Tabla 3.2**) tal y como ocurre en sitios donde el crecimiento está limitado por las bajas temperaturas (Keenan et al., 2013; Madrigal-González et al., 2015). En cualquier caso, la baja sensibilidad del haya al clima que hemos encontrado concuerda con estudios recientes que muestran una gran adaptación al clima local de las poblaciones meridionales del haya (Cavin and Jump, 2017; Muffler et al., 2020; Tegel et al., 2014).

7.2.2. Eventos climáticos extremos

Aunque una determinada especie muestre baja sensibilidad a las fluctuaciones del clima debido a que está creciendo en unas condiciones climáticas favorables, los eventos climáticos extremos (como las sequías y la heladas tardías) que ocurren ocasionalmente pueden producir grandes alteraciones del crecimiento o incluso cambios en la dinámica del bosque (Martin-Benito and Pederson, 2015; Pederson et al., 2014). Este es el caso de los hayedos estudiados en este trabajo que, aunque sus crecimientos están débilmente relacionados con el clima, muestran grandes caídas durante los años de sequía o con heladas tardías.

En Picos de Europa hubo grandes caídas en el crecimiento del haya los años 1923, 1945 y 1995. Al no tener un registro de los años en los que ocurrieron heladas tardías para este sitio, no podemos distinguir entre efectos de heladas y de sequía. Como se vio en la discusión del capítulo 6 (sección 6.4.1), hay una relación directa entre las altas temperaturas, que conducen a una fenología temprana, y los daños causados por las heladas, lo que puede llevar a confundir los efectos de las heladas tardías con los de las sequías y a sacar conclusiones erróneas sobre los factores que controlan el crecimiento cuando se desconocen los años en los que ocurrieron heladas tardías. En este caso es posible que haya una mezcla de ambos fenómenos, con efectos similares sobre el arbolado. Mientras que los años 1945 y 1995 son especialmente calurosos y secos (lo cual no implica que no haya ocurrido una helada tardía), el mes de abril de 1923 fue especialmente frío y pudo haberse producido alguna helada tardía (**Tabla 2.2**). En los años en los que se dieron estos eventos climáticos extremos el haya redujo su crecimiento a la mitad (**Fig. 2.5**), no produciéndose nada de crecimiento en un 20-30% de los árboles (**Fig. 2.E.1**, en los apéndices del capítulo 2), e igualmente se vio reducido el crecimiento en los años posteriores. Durante estos años el haya tuvo una respuesta similar a la del abedul (aunque en esta especie hubo más pies que no crecieron durante esos años) con una resistencia y resiliencia del crecimiento menor que la del roble.

En El Hayedo de Montejo, donde sí se tiene un registro de los daños causados por heladas tardías desde 1994, las mayores caídas del crecimiento se dan en estos años (**Figs. 6.3** y **6.6**). Aquí la especie que vio su crecimiento más afectado por los eventos climáticos extremos fue el haya, la especie de brotación más temprana, llegando reducirse éste hasta en más del 75% en el año de la helada (**Figs. 5.6** y **6.4**) y en un 40% el año siguiente al de la helada (**Fig. 5.C.1**, en los apéndices del capítulo 5, y **Fig. 6.4**). Además del crecimiento, las heladas tardías provocaron un retraso en la foliación, especialmente de las hayas que ya estaban brotando en el momento de producirse la helada y que se ven obligadas a producir una segunda cohorte de hojas, pero también, aunque en menor medida, de aquellas que todavía no habían brotado en dicho momento (**Fig. 5.4**). También se produjo un retraso en la senescencia de las hojas (**Figs. 5.7** y **6.7**), resultado que concuerda con trabajos previos según los cuales

los retrasos en la brotación pueden producir retrasos en la senescencia (Fu et al., 2014; Keenan and Richardson, 2015; Liu et al., 2016; Signarbieux et al., 2017; Zohner et al., 2018). Este retraso en la senescencia además podría afectar también a los años inmediatamente posteriores a las heladas (**Fig. 6.7**). Por otro lado las hayas que perdieron la primera cohorte de hojas debido a las heladas, generaron en la segunda cohorte unas hojas de menor superficie y grosor y menor concentración de hidratos de carbono (**Tabla 5.2**; ver también St. Clair et al., 2009) producto de una menor capacidad fotosintética (Rodríguez-Calcerrada et al., 2008). Los trabajos presentados en el capítulo 5 y 6 son los primeros estudios científicos en los que se muestra que el efecto de las heladas tardías, tanto sobre el crecimiento como sobre la fenología, se puede alargar durante más de un año en el haya.

Hay grandes diferencias en las reducciones del crecimiento mostradas por el haya tras cada una de las heladas. Estas diferencias en el daño recibido parecen estar relacionadas con el clima previo a la helada y el estado fenológico de las hojas en el momento en el que ésta ocurre. Así, en años con un invierno caluroso se adelantaría la brotación (Vitasse et al., 2009) y, en el momento de producirse la helada, habría un mayor número de yemas brotadas, lo que aumentaría el daño recibido por los árboles (ver sección 6.4.1). Sin embargo, estas conclusiones se han obtenido de estudiar 4 heladas tardías ocurridas en fechas similares de años diferentes. Para confirmarlas es necesario realizar un estudio más amplio con un mayor número de haladas tardías y mayor variabilidad en la fecha en la que se dieron las heladas.

La reducción del crecimiento producida en el haya durante lo eventos climáticos extremos, mucho mayor que la que se da en los robles con los que cohabita, ha sido explicada en algunos estudios con la hipótesis de que el haya, durante estos años, predomina el almacenamiento sobre el crecimiento (Dietze et al., 2014; Miranda et al., 2020; Wiley et al., 2017). Según esta hipótesis la reducción en el crecimiento no implicaría un mayor daño sino el efecto de una estrategia conservadora en la que se aumenta la cantidad de nutrientes almacenados para superar posibles perturbaciones futuras. Sin embargo, la helada tardía apenas afectó a las concentraciones de hidratos de carbono de las especies estudiadas (**Fig. 5.5**). El hecho de que la cantidad de hidratos de carbono no parece ser un limitante para el desarrollo de los árboles (Hoch

et al., 2003; Körner, 2003) unido a que los robles albares afectados por la helada apenas vieron alterado su crecimiento o sus concentraciones de hidratos de carbono (**Figs. 5.5** y **5.6**), indica que el haya realmente se vio más afectada por el impacto de estos eventos climáticos.

Los eventos climáticos extremos están asociados con eventos de mortalidad del arbolado (Bigler et al., 2007; Pederson et al., 2014). En Picos de Europa alrededor del 90% de las liberaciones o reducciones de la competencia (aumentos significativos del crecimiento relacionados generalmente con la mortalidad de algún pie vecino) se dieron en los años siguientes a cada evento (**Fig. 2.6**). Al igual que en otros estudios previos (Bigler et al., 2007), hubo una demora de entre 6 y 11 años entre el evento climático y la liberación (**Fig. 2.7**) debido a que estos acontecimientos generalmente no matan directamente al árbol, sino que lo debilitan, predisponiéndolo al ataque de insectos o patógenos que son los que, finalmente, matan al árbol a los pocos años (Bréda et al., 2006). Al morir el árbol se reduce la competencia sobre los pies vecinos lo que deriva en un aumento en el crecimiento de éstos. Aunque no conocemos las especies más afectadas por esta mortalidad, el hecho de que el haya sea junto con el abedul la especie con mayores reducciones del crecimiento durante y tras los eventos climáticos extremos, unido a su susceptibilidad de sufrir fallo hidráulico (Aranda et al., 2005), indican que estas especies posiblemente fueron la que más mortalidad sufrieron.

7.2.3. Competencia

Los cambios de espesura, derivados por un lado de la dinámica natural de la masa y por otro de la gestión o falta de ella, no parecen afectar significativamente al crecimiento de las hayas dominantes o codominantes (**Tabla 4.4**) debido a su gran capacidad para crecer con elevada competencia. El haya generalmente presenta una mayor capacidad competitiva que otras especies con las que se mezcla (Hein and Dhôte, 2006; Manso et al., 2015), aunque esta puede variar según cambian los factores ambientales, especialmente el clima (Weber et al., 2008). Tanto en Picos de Europa como en El Hayedo de Montejo se alternaron periodos donde el haya o los robles con

los que se mezcla mostraron una mayor capacidad competitiva (**Figs. 3.5** y **4.6**). Sin embargo, la evolución de la capacidad competitiva fue diferente en ambas poblaciones. En la población más septentrional la capacidad competitiva del haya muestra una tendencia decreciente, con un gran aumento de los años donde la capacidad competitiva del roble albar es mayor a partir de 1960, en concordancia con el declive del crecimiento del haya asociado al cambio climático encontrado en estudios previos (Bontemps et al., 2010; Braun et al., 2010; Dittmar et al., 2006; Kint et al., 2012; Piovesan et al., 2008) junto con un aumento del crecimiento del roble albar (Becker et al., 1994; Bergès et al., 2000; Kint et al., 2012). Por el contrario, en la población meridional la mayor capacidad competitiva del haya, respecto al roble albar, se mantiene más o menos constante. En ambas poblaciones hay una relación significativa de la capacidad competitiva con el clima (**Tablas 3.3** y **4.3**). Siendo la tendencia del clima similar en los dos lugares de estudio (**Figs. 2.1** y **4.2**), lo esperable hubiese sido encontrar respuestas similares en las dos poblaciones. Sin embargo, la evolución y la edad de la masa son muy diferentes en ambos casos y, tal como se discutió en el capítulo 6 (sección 6.4.2), estas diferencias pueden ser determinantes en la respuesta del crecimiento. Por otro lado estos resultados pueden estar relacionados con la menor sensibilidad y mayor resistencia, en sentido amplio, a la sequía que muestran las poblaciones de haya situadas en su límite de distribución meridional en comparación con las situadas en el centro del área de distribución de la especie (Cavin and Jump, 2017; Serra-Maluquer et al., 2019). Esta mayor resistencia puede explicarse por factores ambientales locales favorables (por ejemplo la topografía o la capacidad de retención de agua del suelo) o por la aclimatación a la sequía (Rodriguez-Calcerrada et al., 2010).

7.2.4. Dinámica de la masa

Las dos masas de haya estudiadas se encuentran en dos momentos diferentes de una misma dinámica que estaría compuesta por las siguientes fases: (i) periodo de gran influencia antrópica con alta presión ganadera y cortas para maderas y leñas. La masa muestra una espesura defectiva con escaso regenerado y pies de gran tamaño. En esta

fase se verían beneficiados los robles por su mayor capacidad para brotar de cepa y el mayor valor de su fruto para el ganado y de su madera para leña. (ii) Fase de densificación tras la reducción de la presión antrópica. La masa, en cuanto a distribución de edades, muestra un estrato viejo e irregular (variabilidad elevada de edades), formado por los pies que ya estaban asentados en la fase anterior, y un estrato inferior y homogéneo (edades similares entre pies), producto del regenerado establecido tras la reducción de la presión ganadera. La estructura diamétrica de la masa es irregular, siendo la representación de la frecuencia de las edades similar a una exponencial negativa (Vélez Olalde, 2016). En esta fase comienza a producirse la mortalidad de algunos individuos por el exceso de espesura (aumenta la espesura, pero disminuye la densidad), pero éstos son dominados y de pequeño tamaño y el hueco que dejan es ocupado por los más próximos. Es en esta fase en la que se encuentra El Hayedo de Montejo (ver sección 4.2.1). (iii) Fase de dinámica de huecos que se caracteriza por perturbaciones a pequeña escala en el dosel del bosque ya maduro, donde un solo árbol o un pequeño grupo de éstos muere, creando un hueco que en función de su tamaño puede propiciar la regeneración (Runkle, 1985). En esta fase se encuentra el hayedo de Picos de Europa (ver sección 3.4.1). La muerte de los árboles puede estar relacionada con múltiples factores bióticos (tamaño del árbol, competencia, enfermedades, plagas, etc.) y abióticos (tormentas, sequías, topografía, suelo, etc.) (McCarthy, 2001), estando relacionada en Picos de Europa con los eventos climáticos extremos (**Fig. 2.7**). La generación de huecos sería un proceso continuo y semipermanente (Lewis and Lindgren, 2000) que se mantendría hasta la ocurrencia de alguna gran perturbación.

Aunque los huecos generados parece que se deben fundamentalmente a la mortalidad del haya y del abedul, por ser más sensibles a los acontecimientos climáticos extremos, y aunque estos huecos parece que son de suficiente tamaño para que se establezcan todas las especies arbóreas que coexisten en la masa (**Fig. 2.8**), la especie más favorecida por este tipo de dinámica es también el haya por su mayor tolerancia a la sombra y su mayor producción de semillas (Harmer, 1994), que le permiten llegar a los sitios con mejor calidad de suelo, reemplazando finalmente a las especies con las que compite (Petritan et al., 2017; Rohner et al., 2012). En este

sentido, cuando la masa de Picos de Europa estaba sometida a una fuerte influencia antrópica, apenas se establecían nuevas hayas, pero una vez que esta presión disminuyó, el establecimiento de hayas aumentó considerablemente mientras que el del roble se mantuvo a niveles similares a los de antes del cambio de uso (**Fig. 3.2**). Igualmente en El Hayedo de Montejo la densificación del arbolado ha hecho que el haya domine en el estrato inferior (regenerado y pies con menores diámetros) sobre el roble albar y el rebollo (Vélez Olalde, 2016).

A pesar del aumento de las temperaturas y la aridificación y de la mayor sensibilidad del haya a los eventos climáticos extremos, no es esperable que se produzca una reversión de la dinámica natural tendente al predominio del haya. De hecho el haya está actualmente en expansión en España y su límite de distribución actual se debe a factores históricos y no a climáticos (Sánchez de Dios et al., 2020, 2016).

7.3. Roble albar

7.3.1. Relaciones entre el crecimiento y el clima

Las variables climáticas explicaron menos variabilidad del crecimiento del roble albar que en el caso del haya (**Tablas 3.2** y **4.4**), indicando una menor sensibilidad al clima del primero. Sin embargo, mientras que en la población más septentrional (Picos de Europa) no muestra relaciones significativas con el clima para el periodo 1980-2013 (**Fig. 2.3**), en la población de Montejo de la Sierra se muestra sensible a las altas temperaturas y las bajas precipitaciones (**Figs. 4.4** y **4.5**). Estas diferencias no estarían relacionadas con las diferencias climáticas entre ambos sitios, sino con las diferencias en edad, espesura y estructura de la masa, las cuales condicionan la sensibilidad del crecimiento al clima (Fernández-de-Uña et al., 2015; González de Andrés et al., 2018; Linares et al., 2010; Martín-Benito et al., 2011; Rozas et al., 2009).

7.3.2. Eventos climáticos extremos

El roble albar mostró, en general, mayor resistencia del crecimiento que el haya y el abedul a los eventos climáticos extremos y, en aquellos años en los que se han producido las mayores caídas del crecimiento, también mostró mayor resiliencia que el haya (**Figs. 2.5** y **6.4**). Según estudios previos el roble albar es menos vulnerable que el haya a la sequía (Aranda et al., 2005, 2000) y según nuestros resultados también es menos vulnerable a las heladas tardías. Por un lado, la brotación del roble albar es en general posterior a la del haya, lo que hace que se vea menos afectado por las heladas, es decir, en el momento de ocurrir una helada tardía el roble tendrá menos yemas brotando que el haya y por tanto sufrirá un daño menor (**Fig. 6.2**). Por otro lado, los robles albares resisten mejor los daños de las heladas tardías. En efecto, aunque las heladas tardías retrasan el momento de la brotación respecto a un año normal, este retraso se debe únicamente a los factores internos que controlan la fenología del árbol (Tedla et al., 2020) y no al daño recibido, de forma que, tanto los robles que han sido dañados por la helada, como aquellos no dañados, brotaron (la segunda y la primera y única cohorte de hojas, respectivamente) simultáneamente tras la helada tardía (**Fig. 5.4**). Además, no se encontraron diferencias significativas, entre los robles albares dañados y no dañados por las heladas, en las concentraciones de hidratos de carbono ni en las características de las hojas (**Tabla 5.2** y **Fig. 5.5**). Todo ello hace que los robles dañados y no dañados puedan mantener unas mismas tasas de crecimiento (**Figs. 5.6** y **5.C.1**, en los apéndices del capítulo 5), por lo que las caídas del crecimiento que se dan durante los años en los que ha habido helada tardía (**Fig. 6.3**) serían un producto indirecto del retraso fenológico que afecta a todos los pies (incluidos los que no han recibido ningún daño en las hojas) antes que del propio daño.

7.3.3. Competencia

En El Hayedo de Montejo de la Sierra, donde ha habido una tendencia al aumento de las temperaturas paralelo a un aumento de la competencia como consecuencia del abandono de los usos tradicionales, la espesura se ha mostrado como el factor más limitante para el crecimiento del roble albar a largo plazo, siendo el clima un factor secundario, aunque también significativo (**Fig. 4.8**). Hay abundancia de estudios que

priman el clima como factor para entender los procesos de decaimiento del crecimiento (Charru et al., 2017; Dorado-Liñán et al., 2019; Piovesan et al., 2008), pero éstos no suelen considerar la evolución de la competencia, normalmente debido a que es una información más difícil de obtener y que se desconoce en la mayoría de los bosques. Sin embargo, cuando se tiene en cuenta la evolución de la competencia, ésta suele explicar casi toda la variación del crecimiento a largo plazo (Foster et al., 2016; Gómez-Aparicio et al., 2011; Liang et al., 2019; Rozas, 2014; Vayreda et al., 2012).

Mientras que en Montejo los periodos de tiempo en los que la capacidad competitiva del roble albar fue superior a la del haya fueron solo el 33% del total (**Fig. 4.6**), en Picos de Europa supusieron el 46% para todo el periodo estudiado y el 64% para el periodo 1960-2013 (**Fig. 3.5**). Por otro lado, la capacidad competitiva del roble albar en Montejo fue, en términos generales, ligeramente superior a la del rebollo. La menor capacidad competitiva del roble frente al haya en Montejo estaría relacionada con el efecto del aumento de la competencia sobre el crecimiento del roble albar. En cuanto a Picos de Europa, el aumento de la capacidad competitiva del roble frente al haya se debe al fuerte aumento del crecimiento en el roble en el periodo 1960-1980 y el estancamiento posterior, frente al estancamiento del crecimiento del haya para este mismo primer periodo y el decaimiento posterior (**Fig. 2.2**) posiblemente relacionado con el aumento de las temperaturas (Bontemps et al., 2010; Braun et al., 2010; Dittmar et al., 2006; Kint et al., 2012; Piovesan et al., 2008). En estos resultados, contradictorios entre ambos estudios, posiblemente tenga una gran influencia las grandes diferencias en edad y estructura de ambas masas, o aspectos edáficos no considerados. Es necesario realizar investigaciones adicionales que determinen la influencia de estos factores en el comportamiento del crecimiento y la capacidad competitiva de cada una de las especies.

7.3.4. Dinámica de la masa

Como ya se ha tratado en la sección 9.2.4 referente al haya, la dinámica natural en los bosques con especies típicas de zonas templadas como el de Picos de Europa o El Hayedo de Montejo es la dinámica de huecos (**Fig. 2.8**), que a largo plazo favorece al

haya, que acaba desplazando al resto de especies menos tolerantes a la sombra con las que compite. En este sentido, el crecimiento del roble albar se mostró mucho menos sensible a la mortalidad del arbolado del vecindario, produciéndose muchos menos aumentos del crecimiento y de menor magnitud que en las hayas (**Fig. 2.6**; ver también Nowacki and Abrams, 1997; Petritan et al., 2017; Rozas, 2004). De modo que el haya se vería más favorecida por los huecos al responder de forma más flexible a la disminución de la competencia del vecindario.

Allí donde compite con el haya, la dinámica natural de la masa acabará relegando al roble albar a los bordes del bosque y sus zonas de expansión, donde la competencia es menor (**Fig. 3.E.1**, en los apéndices del capítulo 3). Sin embargo, allí donde compite con el rebollo, el roble albar, al ser más tolerante a la sombra, podría terminar reemplazándolo. En este sentido, la competencia fue menos influyente sobre el crecimiento del roble albar, que la resistiría mejor, que sobre el rebollo (**Tabla 4.4** y **Fig. 4.8**). En cualquier caso, las diferencias en tolerancia entre ambas especies no parecen determinantes (Rodríguez-Calcerrada et al., 2010) y, por otro lado, la hibridación frecuente entre estos *Quercus* hace más difícil o lento el reemplazo de una especie por otra (Valbuena Carabaña, 2006).

7.4. Rebollo

7.4.1. Relaciones entre el crecimiento y el clima

El rebollo mostró las relaciones más débiles (en relación a las especies con las que cohabita) entre el crecimiento y el clima, lo que indicaría que se encuentra mejor adaptado al clima en Montejo de la Sierra. Aunque mostró altas correlaciones con el clima, incluso mayores que el haya (**Tabla 4.2** y **Figs. 4.4** y **4.5**), al modelizar el crecimiento el rebollo fue la especie menos influida por el clima (**Tabla 4.4**). En efecto, el clima explica la variabilidad interanual del crecimiento en el rebollo, que además es menor en comparación con la variabilidad de las otras especies (**Fig. 4.3**), pero no explica nada de la variación a largo plazo del crecimiento (**Fig. 4.8**).

7.4.2. Eventos climáticos extremos

El rebollo también mostró una mejor adaptación a los eventos climáticos extremos en comparación con las otras especies con las que cohabita. El rebollo de El Hayedo de Montejo no sufre ninguna caída significativa del crecimiento ya sea por sequías o por heladas tardías (**Figs. 6.3** y **6.5**). La ausencia de efecto de las heladas tardías está relacionada con su brotación tardía (**Figs. 6.2** y **6.S.1**, en el material suplementario del capítulo 6), precisamente una adaptación de su fenología a estos sucesos (Körner et al., 2016; Lenz et al., 2013; Vitasse et al., 2018).

7.4.3. Competencia

El crecimiento del rebollo en El Hayedo de Montejo está decayendo desde los años 90 (**Fig. 4.3**) debido al aumento de la competencia, producto de la prohibición del pastoreo y las cortas (**Tabla 4.4** y **Fig. 4.8**). Esta especie es, además, la que muestra menores tasas de crecimiento (**Fig. 4.3**) a pesar de su mayor edad (**Tabla 4.1**) y tamaño medio (ver sección 4.2.1). Debido al efecto de la espesura sobre el rebollo, esta especie fue la que mostró una menor capacidad competitiva a lo largo de todo el periodo estudiado en Montejo, menor que el roble albar y sobre todo menor que el haya (**Fig. 4.6**). El área basimétrica de *Q. pyrenaica* se muestra como el principal factor limitante del crecimiento del roble albar y del propio rebollo (**Tabla 4.4**), por encima del efecto que produce el área basimétrica de *F. sylvatica*, una de las especies que más presión ejerce sobre aquellas con las que convive (Hein and Dhôte, 2006; Manso et al., 2015), sin embargo en este caso hay que considerar que el rebollo tiene los mayores diámetros medios (ver sección 4.2.1) y que la competencia depende directamente del tamaño del competidor (Contreras et al., 2011). Por tanto este mayor efecto del rebollo se debería a su mayor tamaño.

7.4.4. Dinámica de la masa

La dinámica de la masa que hay en El Hayedo de Montejo, que es de huecos causados por mortalidad de árboles aislados, favorece el desarrollo del roble albar y, principalmente, del haya frente al rebollo, tanto por la menor tolerancia del rebollo a la competencia, que ha provocado el decaimiento de su crecimiento en las últimas décadas (**Figs. 4.3** y **4.8**), como por su menor tolerancia a la sombra (Niinemets and Valladares, 2006; Rodríguez-Calcerrada et al., 2010). El rebollo estaría mejor adaptado al clima, siendo mucho menos sensible a los eventos climáticos extremos que el roble y sobre todo el haya. Sin embargo, la mayor adaptación al clima no parece que sea un factor lo suficientemente importante como para revertir este fenómeno. De hecho, en términos generales, el haya domina actualmente el estrato inferior (regenerado y pies con menores diámetros) de este bosque (Vélez Olalde, 2016). Si aumentase la frecuencia e intensidad de las sequías y las heladas tardías, por efecto del cambio climático, el rebollo se vería beneficiado por su mayor resistencia frente a estos eventos.

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CAPÍTULO 8. CONCLUSIONES GENERALES Y SUS IMPLICACIONES PARA LA SELVICULTURA

Entendida la resiliencia en su acepción más general, como la capacidad de un ecosistema para permanecer en el tiempo adaptándose a los cambios del ambiente, las masas estudiadas mostraron una gran resiliencia. En ninguna de ellas se detectó un decaimiento en el crecimiento que se debiera fundamentalmente a razones climáticas. Igualmente, aunque los eventos climáticos extremos pueden llegar a ocasionar la muerte de algunos individuos en los bosques templados caducifolios, esta mortalidad se produce de forma espacialmente dispersa, contribuyendo a la dinámica de huecos típica de estos ecosistemas.

En los bosques estudiados se encontró una buena adaptación al clima de todas las especies. El haya y el abedul mostraron una mayor sensibilidad a los eventos climáticos extremos, especialmente las heladas tardías en el caso del haya. El roble albar y el rebollo se ven afectados fundamentalmente por el aumento de la competencia, la cual es la responsable del declive del crecimiento que se ha encontrado en estas dos especies, especialmente en el rebollo.

La capacidad competitiva estimada mediante el incremento en crecimiento relativo es diferente entre estas especies y también varía a lo largo del tiempo, en función de las condiciones ambientales. En Picos de Europa en las últimas décadas el roble albar ha mostrado una mejor capacidad competitiva frente al haya, posiblemente gracias al aumento de las temperaturas. Sin embargo, en El Hayedo de Montejo el haya ha mostrado una mayor capacidad competitiva a lo largo de todo el periodo estudiado.

Picos de Europa y el hayedo de Montejo de la Sierra se encuentran en distintas fases de una misma dinámica de la masa a largo plazo, en la que el haya desplaza al resto de especies en las zonas de bosque denso, por su temperamento tolerante, a las zonas de expansión del bosque y suelos someros.

El posible aumento de los eventos climáticos extremos y la mayor sensibilidad a los mismos del haya, hace recomendable, para aumentar la estabilidad del ecosistema, la aplicación en Picos de Europa y en El Hayedo de Montejo de las técnicas selvícolas que garanticen el mantenimiento de una masa mixta, abriendo claros del suficiente tamaño para permitir la instalación de las otras especies y disminuyendo la competencia cuando sea necesario para permitir las ascensión al estrato dominante de las especies menos tolerantes a la sombra.

General conclusions and their implications for silviculture

The studied forest ecosystems showed great resilience, that is, capacity to remain in time by adapting to environmental changes. The climate does not constitute the main driver of growth decline in *Picos de Europa* or *El Hayedo de Montejo*. Likewise, although extreme climatic events may cause the death of some individuals in temperate deciduous forests, this mortality occurs scattered, contributing to the gap dynamics typical of these ecosystems.

In the studied forests, all species were well adapted to climate. *F. sylvatica* and *B. pubescens* showed higher sensitivity to extreme climatic events, especially late frosts in the case of *F. sylvatica*. *Q. petraea* and *Q. pyrenaica* are mainly affected by the increase of competition, which is responsible for the growth decline found in these two species, especially in *Q. pyrenaica*.

The competitive capacity, estimated by the relative growth increment, is different among species and also varies over time, depending on environmental conditions. In *Picos de Europa* in the last decades *Q. petraea* has shown a greater competitive capacity than *F. sylvatica*, possibly thanks to the temperature increase. However, in *El Hayedo de Montejo F. sylvatica* has shown a greater competitive capacity than *Q. petraea* and *Q. pyrenaica* throughout the whole period studied.

Picos de Europa and *El Hayedo de Montejo* are in different phases of the same long-term forest dynamic, in which *F. sylvatica* displaces the other species in dense forest areas, due to its tolerant temperament, to areas of forest expansion and shallow soils.

The possible increase in extreme climatic events and the greater sensitivity of *F. sylvatica* to them, makes advisable, in order to increase the resilience of the ecosystem, the application in *Picos de Europa* and in *El Hayedo de Montejo* of silvicultural traits that guarantee the maintenance of a mixed forest, favoring the regeneration of *Q. petraea* or *Q. pyrenaica* and reducing competition to allow the less shade tolerant species to ascend to the dominant stratum.